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STONEFLIES (PLECOPTERA) OF THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING, USA: DISTRIBUTION AND ZOOGEOGRAPHIC AFFINITIES

Bret O. Huntsman[1], Richard W. Baumann[1,2], and Boris C. Kondratieff[3]

ABSTRACT.—The Black Hills of South Dakota and Wyoming are an insular mountain range completely surrounded by the Great Plains. The stonefly (Plecoptera) fauna of the Black Hills was surveyed and zoogeographic affinities examined. Twenty-seven species representing 22 genera and 6 families were found. Fifteen new state records for South Dakota and 2 for Wyoming are presented. Two species are removed from the South Dakota list. An analysis of the North American distribution of each species showed a strong relationship between the Black Hills and the Rocky Mountains, with much weaker relationships between the Black Hills and eastern and northern regions. Results of a logistic regression analysis comparing factors contributing to long-distance dispersal ability against presence/absence in the Black Hills were inconclusive. However, other evidence suggests that the Black Hills fauna is a result of expansion and subsequent vicariance of stonefly populations during Pleistocene climatic oscillations.

Key words: stoneflies, Plecoptera, zoogeography, Black Hills, South Dakota, Wyoming, Pleistocene.

The Black Hills are an island of mountains in a sea of grass (Turner 1974). These isolated mountains, located in western South Dakota and eastern Wyoming, are completely surrounded by the Great Plains physiographic region. The Black Hills contain one of the most unusual mixes of biotic affinities in North America. For example, 30% of the plant species found in the Black Hills have Rocky Mountain affinities, 9% have eastern deciduous forest affinities, 6% have northern boreal forest affinities, while the remainder are a mix of steppe and widespread species (Hayward 1928, McIntosh 1931, Van Bruggen 1985). Mammal species of the Black Hills show similar mixed affinities. Approximately 14.3% are Rocky Mountain, 8.6% are from eastern deciduous forests, 14.3% are from northern boreal forests, and the rest are a mix of widespread, steppe, and Sonoran species (Turner 1974). Insects in the Black Hills also appear to have mixed affinities. For instance, the mayfly (Ephemeroptera) fauna of the Black Hills has western species (36.8% of the fauna), eastern species (21.1%), and widespread species (42.1%) (McCafferty 1990).

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Another interesting aspect of Black Hills biogeography is the fact that many populations of plants and animals inhabiting the area are highly disjunct, being separated from the nearest conspecific populations by as much as 600 km (Turner 1974, Van Bruggen 1985, McCafferty 1990). These disjunct populations also often represent the extreme range limit for their species (Turner 1974, Van Bruggen 1985, McCafferty 1990).

The most common hypothesis explaining these striking biogeographic patterns is that these disjunct populations are vicariated relicts from the most recent period of glaciation (Ross 1965, Turner 1974, McCafferty 1990). Palynological studies indicate that during the Full-glacial period of the Wisconsin glaciation (30,000–13,000 years BP) much of the central portion of the United States was covered with boreal forest (Wright 1970), allowing typical boreal animals to inhabit this region. This cooler, wetter climate also allowed deciduous gallery forests to form along stream banks, providing avenues of expansion for eastern deciduous forest species into the Black Hills (Turner 1974). Later, during the Late-glacial period (13,000–10,500 BP), the boreal forest followed the retreating ice sheet and was replaced by steppe habitat in the Great Plains (Hoffman and Jones 1970). Eastern and northern species that had expanded into the Black Hills during the Full-glacial period were then isolated in the refuge formed there by the remnant deciduous and boreal forests (Turner 1974).

Also during the Full-glacial period of the Wisconsin the cordilleran-montane zone of the Rocky Mountains was depressed about 1200–1400 m. This displaced the biota of this zone eastward, extending from the Laramie and Big Horn Mountains of Wyoming into the Black Hills (Turner 1974). Again, when the ice sheet retreated, the montane species that had expanded into the Black Hills were isolated in the refuge formed there (Turner 1974).

Although the hypothesis of Ross (1965), Turner (1974), and McCafferty (1990) has great explanatory power, it is not the only possibility. It is also possible that the Black Hills populations of plants and animals were established via long-distance dispersal. Sometime after the formation of the Great Plains, various species may have dispersed across it and founded populations within the Black Hills. At the present time no quantitative studies have been performed comparing vicariance and dispersal models for the Black Hills fauna.

Faunal affinities and distribution histories are most easily studied using organisms restricted to definable habitats (Sargent et al. 1991, Houseman and Baumann 1997). One outstanding example of this type of organism is the insect Order Plecoptera (stoneflies). Most stonefly species require cold, clean streams with rocky streambeds to complete their life cycles (Surdick and Gaufin 1978, Ward 1984, Stewart and Stark 1988). Adult stoneflies are not powerful fliers and usually are not capable of long-distance migrations (Ross 1965, Hynes 1988, Marden and Kramer 1994, Griffith et al. 1998). Thus, dispersal of most stonefly species is thought to require adequate water connections (Surdick and Gaufin 1978, Baumann 1979, Flanagan and Flanagan 1982). Many species have restricted ranges, and distinct differences exist between the stonefly faunas of western, eastern, and northern North America, primarily at the generic and/or specific levels (Ricker 1964, Dosdall and Lemkuhl 1979, Stark et al. 1986).

Few published records are available on the stoneflies of the Black Hills. Presently, only 14 species have been reported from the Black Hills region (Stark and Gaufin 1976, Baumann et al. 1977, Stark et al. 1986). Several families, such as the Capniidae, Pteronarcyidae, Taeniopterygidae, and Leuctridae, have not been previously reported from the Black Hills. Unfortunately, many of the streams within the Black Hills have been affected by pollution and other perturbations (Stewart and Thilenius 1964). It is possible that some populations of stoneflies within the Black Hills have already been extirpated. In the face of the current challenge to document North American biodiversity (Kosztarab and Schaefer 1990), inventorying the stonefly fauna of the Black Hills should be a priority.

Our study had 3 main objectives: to document the stonefly fauna of the Black Hills, to determine if the stoneflies of this region reflect the mixed affinities shown by other groups of organisms, and to quantitatively test the vicariance hypothesis of Ross (1965), Turner (1974), and McCafferty (1990) using these new stonefly distributional data.

STUDY AREA

The Black Hills region consists of the Black Hills proper and the Bear Lodge Mountains in western South Dakota and northeastern Wyoming (approximately 43°10′–44°50′ N lat., 103°20′–104°50′ W long.; Turner 1974). The Black Hills were created by intermittent domal uplifts during the Cretaceous, Miocene, and Pleistocene (Turner 1974). Elevations in the Black Hills region range from 1000 m on the western plains to 2228 m at Harney Peak. The area is completely surrounded by the Northern Great Plains physiographic province, which consists of arid to semiarid short grass prairie (Fig. 1). The Black Hills are located approximately 240 km east and northeast of the Big Horn and Laramie ranges of the Rocky Mountains, respectively. The nearest component of northern boreal forest is in Saskatchewan, approximately 600 km to the north. The nearest component of eastern deciduous forest is in Minnesota, approximately 600 km to the east, although gallery forests exist along the Missouri River, approximately 200 km to the east. The Black Hills are drained by the Cheyenne and Belle Fourche rivers, which circle around the southern and northern ends of the Black Hills (Fig. 1). Since these rivers originate in the plains of eastern Wyoming, there are no direct water connections between the Rocky Mountains and the Black Hills. The Belle Fourche drains into the Cheyenne approximately 80 km east of the Black Hills (Fig. 2), which in turn drains into the Missouri River.

METHODS

We made collections at 112 sites within the Black Hills region. These collection sites were chosen to provide coverage of all major drainages and most major creeks and streams within the Black Hills. Although not considered part of the Black Hills proper, the Belle Fourche and Cheyenne rivers were included in our collections because stonefly species have direct water connections to the Black Hills via these drainage systems. Collections were made in February and June 1995, April and August 1996, and July 1997 to include species emerging in the winter, spring, and summer. All specimens collected were preserved in 70% ethyl alcohol.

Adult stoneflies were collected using beating sheets or aerial nets, or by hand. Nymphal stoneflies were collected with aquatic dip nets. At some sites nymphs of selected species were set aside and reared to adults to assist in specific identification. All adults (and the nymphs of certain species) were identified using keys in Baumann et al. (1977) and Stewart and Stark (1988).

In addition to field-collected specimens, we examined specimens from the following institutions: Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah (BYUC); C.P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins (CSUC); Illinois Natural History Survey, Champaign (INHS); North Dakota State University Research Collection, Fargo (NDSU); Purdue Entomological Research Collection, Purdue University, West Lafayette, Indiana (PURC); South Dakota State University Research Collection, Brookings (SDSU); United States National Museum, Smithsonian Institution, Washington, D.C. (USNM); and University of Nebraska Research Collection, Lincoln (UNSM). Specimens collected during the course of this study are deposited in the Monte L. Bean Life Science Museum and C.P. Gillette Museum of Arthropod Diversity.

The North American distribution of each species collected in the Black Hills was examined to determine its region of faunal affinity (Baumann et al. 1977, Stark et al. 1986, Stark 1998). This allowed us to determine probable source pools for species inhabiting the Black Hills. The stonefly faunas of Colorado (Stark et al. 1973, Baumann et al. 1977, Stark et al. 1986), Minnesota (Harden and Mickel 1952, Stark et al. 1986), and Saskatchewan (Dosdall and Lemkuhl 1979, Stark et al. 1986) were initially selected to represent western, eastern, and northern source pools for purposes of a statistical test of the long-distance dispersal model. These areas were chosen both for their proximity to the Black Hills and availability of published records (Baumann et al. 1977, Dosdall and Lemkuhl 1979, Harden and Mickel 1952, Stark et al. 1986).

If the Black Hills were colonized by random, long-distance dispersal flights across the Great Plains, one would expect those stonefly species with greater dispersal abilities to be over-represented in the Black Hills fauna (Houseman and Baumann 1997). We used a logistic regression procedure (PROC LOGISTIC; SAS 1990) to determine if dispersal ability would predict the occurrence of stonefly species in the Black Hills fauna. A significant positive relationship between dispersal ability and presence in the Black Hills would provide evidence that long-distance dispersal is a viable alternative to vicariance as a mode of colonization.

Flying insects can disperse long distances either by active, powered flight (adaptive dispersal) or by being accidentally caught up in convective upcurrents, which deliver them to the stronger winds present at higher altitudes (inadvertent dispersal; Johnson 1969, Drake and Farrow 1988). For purposes of this test we assumed that either type of dispersal could occur. The dispersal ability of all stonefly species occurring in the Black Hills and the hypothesized source pools were quantified based on the following factors: season of emergence, length of emergence, ecological tolerance, and overall distribution in the source range (adapted from Houseman and Baumann 1997). However, due to the low number of eastern and northern species inhabiting the Black Hills (see Results section below), only western species (represented by the Colorado fauna) were tested to determine if dispersal ability predicted presence in the Black Hills. Each species was given a score for each factor based on data published in Baumann et al. (1977) and Baumann (1979). These scores were determined using the following criteria.

SEASON OF EMERGENCE.—Muscle power output of insects is severely restricted at low temperatures (Josephson 1981, Marden and Kramer 1994). Stoneflies are no exception. Even winter-emerging species are sluggish and rarely fly at temperatures near or below freezing (Frison 1929, Marden and Kramer 1994). In addition, during periods of extreme cold, winter stoneflies seek shelter under rocks, bark, and leaves (Frison 1929) and are unlikely to be engaged in dispersal activities. Therefore, we assumed species that emerge in colder months are less likely to successfully disperse. We scored species with September to March emergence as 1, species that emerge from April to June as 2, and those that emerge from July to August as 3.

LENGTH OF EMERGENCE.—We assumed that dispersal is more likely for species with longer emergences for 2 reasons. First, adults are more likely to be present during extended periods of calm weather, which is conducive to adaptive dispersal (Johnson 1969). Second, a longer period of emergence would increase the probability of inadvertent dispersal via convective upcurrent events. Species with adults present for 3 months or less in the source pool were scored 1, those with adults present 4–5 months were scored 2, and those with adults present for more than 5 months were scored 3.

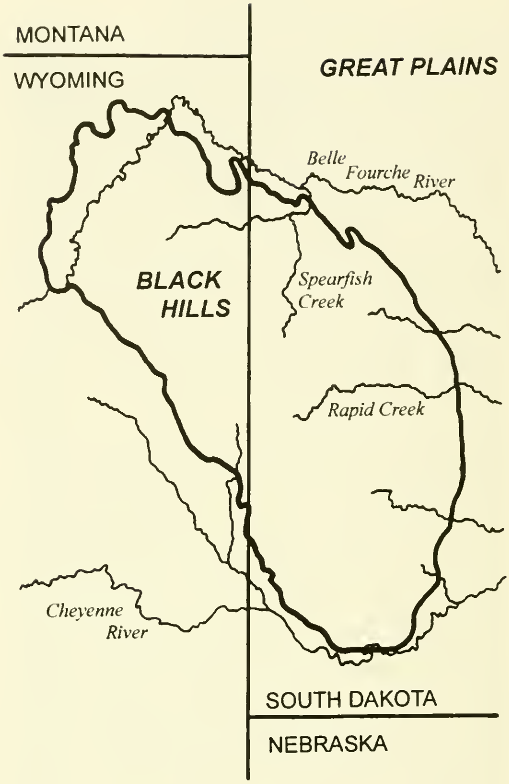

Fig. 1. The Black Hills of South Dakota and Wyoming.

ECOLOGICAL TOLERANCE.—Baumann (1979) identified 3 major stonefly environments (cold lotic, warm lotic, and cold lentic) and the genera which inhabit them. All species in this analysis primarily inhabit cold lotic habitats. However, those that can tolerate warm lotic habitats would be more likely to survive in intervening areas of the Great Plains during dispersal, since cold habitats are rare in the prairies. In addition, warm-tolerant species could more easily colonize the Black Hills upon

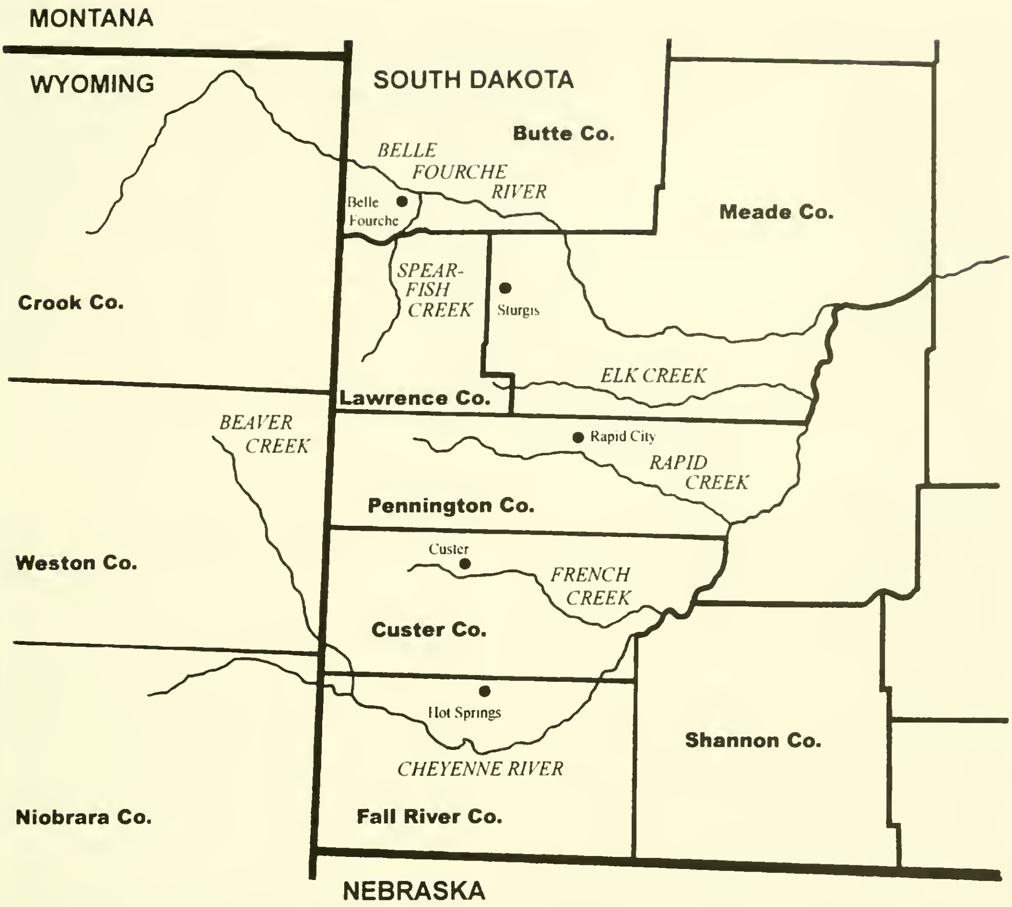
MONTANA
WYOMING
SOUTH DAKOTA
Butte Co.
BELLE FOURCHE RIVER
Belle Fourche
Meade Co.
SPEAR-FISH CREEK
Sturgis
Crook Co.
ELK CREEK
Lawrence Co.
BEAVER CREEK
Rapid City
RAPID CREEK
Pennington Co.
Custer
FRENCH CREEK
Weston Co.
Custer Co.
Hot Springs
Shannon Co.
CHEYENNE RIVER
Niobrara Co.
Fall River Co.
NEBRASKA

Fig. 2. Counties, major cities, and major drainages in the Black Hills region of South Dakota and Wyoming.

arrival, since more habitats would be available for them. Species limited to cold lotic environments were scored 1, while those known from both cold and warm lotic habitats were scored 2 (we omitted cold lentic habitats from our analysis since few species are known from them and few of these habitats exist in the Great Plains).

DISTRIBUTION WITHIN THE SOURCE POOL.—We assumed that species with wider distributions within the source pool possess higher vagility and thus have a higher probability of performing adaptive dispersal flights. Also, those species with wider distributions are more likely to be picked up by local, random convective currents and dispersed by high-altitude winds. The number of Colorado counties in which each species occurs was used to represent overall distribution (range 1–22).

RESULTS

We collected 27 species of stoneflies representing 22 genera and 6 families in the Black Hills region. They are listed in Table 1 by state and county in which they were collected. Fifteen of these species represent new state records for South Dakota, while 2 represent new state records for Wyoming (Table 1).

The winter stonefly genus *Isocapnia* was represented in our study by a single female, designated *Isocapnia* sp. A, collected in 1982. This brachypterous female may represent an undescribed species.

The zoogeographic affinities of the stonefly species in the Black Hills fall into 4 major categories: western (21 species), eastern (2 species), northern (1 species), and widespread (3 species; Table 2). Western species are defined

TABLE 1. Stonefly species of the Black Hills by state and county.

	South Dakota						Wyoming	
Species	Butte	Custer	Fall River	Lawrence	Meade	Pennington	Crook	Weston
Amphinemura banksi		X		X		X	X	X
Malenka coloradensis		X		X		X	X	
*Nemoura trispinosa**,†		X		X		X	X	
*Prostoia besametsa**		X		X		X	X	X
Zapada cinctipes		X		X	X	X	X	X
*Capnia confusa**		X		X		X		
*Capnia gracilaria**		X		X		X		
*Eucapnopsis brevicauda**		X		X		X		
Isocapnia sp. A*				X				
*Paracapnia angulata**				X	X	X	X	
*Utacapnia lemoniana**		X		X		X		
*Paraleuctra vershina**		X		X	X	X		
*Isogenoides elongatus**				X		X		
Isoperla longiseta	X		X				X	
Isoperla phalerata	X	X		X	X	X	X	X
Isoperla quinquepunctata	X	X		X	X	X	X	X
*Isoperla transmarina**,†						X	X	
*Skwala americana**		X		X		X	X	
*Acroneuria abnormis**	X						X	
Claassenia sabulosa				X				
Hesperoperla pacifica		X		X		X	X	X
*Perlesta decipiens**	X		X					
Paraperla frontalis		X		X		X		
*Suwallia lineosa**				X				
Sweltsa borealis				X		X		
Sweltsa coloradensis		X		X		X		
Triznaka pintada		X		X		X	X	X

*indicates new South Dakota state record
†indicates new Wyoming state record

as those whose region of greatest abundance falls west or northwest of the Great Plains, while eastern species are those most abundant east of the Great Plains. Northern species are those occurring primarily in the previously glaciated areas of Canada and the Great Lakes region. Finally, widespread species are those with a largely east–west transcontinental distribution. It is interesting to note that no southern species or endemic species were collected in the Black Hills.

Logistic regression analysis of factors affecting dispersal ability found 2 factors, length of emergence ($\chi^2_1 = 4.28$, $P = 0.038$) and distribution in the source pool ($\chi^2_1 = 6.71$, $P = 0.010$), to be significant predictors of presence in the Black Hills.

DISCUSSION

In his catalog of the world Plecoptera fauna, Illies (1966) listed 3 species from the Black Hills region. Stark and Gaufin (1976) reported *Claassenia sabulosa* (Banks) from Lawrence County. In their review of the stoneflies of the Rocky Mountains, Baumann et al. (1977) treated the Black Hills as an extension of the Rockies. They listed 11 species of stoneflies in the Black Hills. However, they neglected *C. sabulosa*. Stark et al. (1986) listed 14 species from South Dakota. In addition to the 12 species listed by previous authors, Stark et al. added *Isoperla longiseta* Banks and *Triznaka pintada* (Ricker).

Both Baumann et al. (1977) and Stark et al. (1986) list *Nemoura arctica* Esben-Peterson as occurring in the Black Hills. These records were based on a single female collected in 1953 and 2 females collected in 1965. Our subsequent efforts failed to locate any specimens of *N. arctica*, although a congener, *N. trispinosa* Claassen, proved to be common. The 3 females previously identified as *N. arctica* are actually *N. trispinosa*. There appears to be no evidence that *N. arctica* occurs within the Black Hills. In addition, both Baumann et al. (1977) and Stark et al. (1986) list *T. signata* (Banks) from the Black Hills region. Several vials of specimens from the Illinois Natural History Survey containing *T. pintada* from the Black Hills were incorrectly identified as *T.*

TABLE 2. Geographic affinities of the stonefly species of the Black Hills.

WESTERN SPECIES

Amphinemura banksi
Malenka coloradensis
Prostoia besametsa
Zapada cinctipes
Capnia confusa
Capnia gracilaria
Eucapnopsis brevicauda
Isocapnia sp. A
Utacapnia lemoniana
Paraleuctra vershina
Isogenoides elongatus
Isoperla phalerata
Isoperla quinquepunctata
Skwala americana
Claassenia sabulosa
Hesperoperla pacifica
Paraperla frontalis
Suwallia lineosa
Sweltsa borealis
Sweltsa coloradensis
Triznaka pintada

WIDESPREAD SPECIES

Isoperla longiseta
Acroneuria abnormis
Perlesta decipiens

EASTERN SPECIES

Paracapnia angulata
Isoperla transmarina

NORTHERN SPECIES

Nemoura trispinosa

signata. It is probable that these samples represented the errant records reported by these authors.

Analysis of factors affecting dispersal ability showed 2 factors, length of emergence and distribution in the source pool, to be significantly related to presence/absence in the Black Hills. Upon further analysis, however, it appears the significant result for length of emergence is due entirely to low numbers of capniid species in the Black Hills. Only 6 species of capniids have been found in the Black Hills, compared to 20 species in Colorado. In addition, one of the Black Hills species, *Isocapnia* sp. A, could not be included in the original analysis due to lack of specific identification. Therefore, only 5 capniid species from the Black Hills were included in the original analysis. Since most species in the family Capniidae have short emergences (Baumann et al. 1977), a paucity of capniids in the Black Hills could bias the results. To determine if this happened, we repeated the analysis with the species in the family Capniidae removed from the data set. No significant relationship between emergence length and presence in the Black Hills was found among the species of the 5 remaining families ($\chi^2_1 = 1.42$, $P = 0.23$).

There was a significant relationship between distribution in the source pool and presence in the Black Hills even after capniids were removed from the analysis ($\chi^2_1 = 5.36$, $P = 0.021$). This positive result provides some evidence that long-distance dispersal may have been a factor in the origin of the Black Hills fauna, although this evidence is far from conclusive. It is possible to argue that this result would be expected in a vicariance model if the habitat connections before the vicariance event were of short duration or poor quality, since only the most vagile species would then be expected to reach the Black Hills. Thus, the question of mode of origin for the Black Hills fauna was not resolved by this analysis.

A vicariance explanation for the origin of the Black Hills stonefly fauna is supported by the similarity of its distributional pattern (Table 2) to that of mammals, plants, and mayflies (Turner 1974, Van Bruggen 1985, McCafferty 1990). It is unlikely that 4 separate groups, each with very different dispersal modes and abilities, would have similar distributional patterns originating independently via long-distance dispersals. The most parsimonious explanation is that the entire biota was isolated at the same time by a vicariance event, most likely by the formation of the Great Plains at the end of the Pleistocene.

Although the Black Hills stonefly fauna exhibits a pattern of mixed zoogeographic affinities similar to other groups, there are some differences. The percentage of eastern species of stoneflies (7.4%) agrees well with those of plants, mammals, and mayflies (range 8.6–21.1%), while the percentage of northern stoneflies (3.7%) resembles that of other groups (range 0–14.3%; Turner 1974, Van Bruggen 1985, McCafferty 1990). However, the percentage of western species of stoneflies (77.8%) is far higher than the percentage of western species of other groups (range 14.3–31.6%; Turner 1974, Van Bruggen 1985, McCafferty 1990). Also, only 14.8% of the Black Hills stonefly fauna consists of either prairie or widespread species, compared to 42.1–62.8% for other groups (Turner 1974, Van Bruggen 1985, McCafferty 1990). There are few species of stoneflies able to tolerate streams typical of the prairies (Ricker 1946, 1964). This explains the paucity of prairie or widespread stonefly species in the Black Hills. The large number of western species, however, is more difficult to interpret. There are roughly 7 times more western species than eastern and northern species in the Black Hills. This suggests that direct water connections between the Rocky Mountains and the Black Hills during the Wisconsin glaciation were more extensive than connections to the east. This agrees with Pleistocene glacial drainage patterns. During the Pleistocene, the general drainage pattern of the Great Plains consisted of parallel rivers running from the Rocky Mountains to near the glacial boundary (Cross et al. 1986). Here these rivers were deflected to the south by the Laurentide ice sheet, converging to form a large river which flowed southeast to Kansas and Oklahoma (Cross et al. 1986). While Rocky Mountain species had a relatively direct path across the Great Plains to the Black Hills, eastern species had to travel the longer route around the southern tip of the ice lobe to reach the Black Hills. However, this is not the only interpretation. The disparity in the ratio of eastern and western species may also reflect the fact that the prevailing winds in the Black Hills are from the west (Orr 1975), and thus adaptive and inadvertent dispersal flights from the west are more probable.

A total of 27 species of stoneflies is relatively low for an area as large as the Black Hills. In comparison, 37 species of stoneflies have been reported from the Raft River Mountains of Utah, which cover an area only one-tenth as large (Houseman and Baumann 1997). McCafferty (1990) found the diversity of mayflies (Ephemeroptera) in the Black Hills to be low as well. This may reflect a low rate of colonization of the Black Hills by aquatic insects. However, activities by man also may have reduced the diversity of the area. As previously mentioned, most streams in the Black Hills have been heavily impacted by reduced flows, mine drainage, grazing, and agriculture (Stewart and Thilenius 1964). Thus, it is possible that some populations of aquatic insects native to the area have been extirpated. Many stonefly species in the Black Hills have very restricted ranges within the region. Some species, such as *Isoperla transmarina* Newman, *Isogenoides elongatus* (Hagen), *Isocapnia* sp. A, and *Sweltsa lineosa* (Banks), were found in only 1 or 2 streams, suggesting relatively limited populations in the Black Hills. This makes them susceptible to stochastic extinction events.

Of the groups examined in the Black Hills, only 1, the plants, contains an endemic species (Van Bruggen 1985). This single endemic species of plant is a hybrid, meaning it could have arisen very recently. This lack of endemics is unusual for an area as large and isolated as the Black Hills. In comparison, the Ozarks and Ouachita Mountains of the south central U.S. contain 25 endemic species of stoneflies, fully 28% of the stonefly fauna of that region (Poulton and Stewart 1991). Lack of endemics in the Black Hills indicates a young fauna, which lends credence to the assumption that the Black Hills have been isolated ecologically only since the latest period of glaciation.

Due to the isolated location of the Black Hills, most populations of stoneflies in the area represent the extreme range limit for their respective species (15 of 21 western species, 1 of 2 eastern species, 1 of 1 northern species). Also, because of the Black Hills location, almost all stonefly populations in the area are highly disjunct, in some cases being separated by over 600 km from their nearest known conspecific population. This same pattern is exhibited by mammals, plants, and mayflies in this area (Turner 1974, Van Bruggen 1985, McCafferty 1990). The Black Hills is one of the very few places in which the eastern, western, and northern biota overlapped during the Wisconsin glaciation, and which also contained the elevation necessary to provide a refuge from the encroaching steppe for cold-adapted organisms like stoneflies.

One of the most interesting distributional patterns in the Black Hills was exhibited by the 3 species with widespread distributions: *Acroneuria abnormis* (Newman), *Perlesta decipiens* (Walsh), and *Isoperla longiseta*. These 3 species were found only in the Belle Fourche and Cheyenne rivers. As was stated earlier, these rivers are not in the Black Hills proper, but rather surround and drain the area. These 3 species are not montane species and seemed unable to invade the streams of the Black Hills and, other than a single collection of *Isoperla quinquepunctata* (Banks) in the Belle Fourche, no other species in the Black Hills was found in these 2 rivers. This coincides with the sharp contrast between montane and prairie habitats at the edge of the Black Hills. Ward (1984) found that differences in temperature regimes associated with altitude differences appeared to be the controlling variable in Plecoptera diversity patterns in a montane stream in Colorado. This agrees well with our findings in the Black Hills. Cold-adapted, montane species were not found in prairie streams, while the three warm-adapted species were not found in the more montane streams.

CONCLUSIONS

Twenty-seven species of stoneflies from 22 genera and 6 families are reported from the Black Hills region. Twenty-one of the species have western affinities, while 2 are eastern, 1 is northern, and 3 are widespread species. Fifteen species represent new state records for South Dakota and 2 represent new state records for Wyoming. Two species, *Nemoura arctica* and *Triznaka signata*, are deleted from the list of stoneflies of South Dakota.

Results of a logistic regression analysis of dispersal abilities were inconclusive. Although other evidence suggests the stonefly fauna of the Black Hills is the result of expansion and subsequent contraction of eastern, western, and northern stonefly faunas during Pleistocene climatic oscillations, this cannot be verified at the present time.

Lack of endemic species indicates the Black Hills stonefly fauna is relatively young. Low diversity of the stonefly fauna may be the result of low colonization rates (either presently or during the Wisconsin), high extinction rates due to habitat destruction, or both.

ANNOTATED LIST OF STONEFLY SPECIES OF THE BLACK HILLS

To conserve space, full data are not given. These data are available from the authors. Unless otherwise indicated, all specimens listed below are deposited in the Monte L. Bean Life Science Museum at Brigham Young University and in the C.P. Gillette Museum of Arthropod Diversity at Colorado State University. The following symbols are used to represent the type of specimen(s) collected: ♂ = adult male, ♀ = adult female, N = nymphs, and E = exuviae. Adult specimens reared from nymphs are indicated by an asterisk.

Order Plecoptera
Suborder Arctoperlaria
Group Euholognatha
Family Nemouridae

Genus *Amphinemura*
Amphinemura banksi
Baumann and Gaufin

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Flynn Creek, 22-VIII-1996, 1♂; Iron Creek, 22-VIII-1996, 42♂ 23♀; stream entering Sylvan Lake, 23-VIII-1996, 5♂ 4♀; tributary of Beaver Creek, 9-VII-1997, 2♀; Willow Creek, 21-VIII-1996, 20♂ 11♀. *Lawrence Co.:* East Spearfish Creek, 25-VIII-1996, 5♂ 2♀; Elk Creek, 25-VIII-1996, 4♂ 1♀; Hay Creek, 25-VIII-1996, 1♀; Iron Creek, 26-VIII-1996, 6♂ 6♀, 13-VII-1997, 2♂ 1♀; Little Spearfish Creek, 21-VIII-1954, 1♂ 3♀, 15-X-1994, 1N (SDSU), 26-VIII-1996, 12♂ 4♀, 13-VII-1997, 4♂ 4♀; South Fork Boxelder Creek, 25-VIII-1996, 1♂ 2♀, 12-VII-1997, 1♂; South Fork Rapid Creek, 23-VIII-1996, 10♂ 5♀; Spearfish Creek, 27-VII-1940, 5N (INHS), 16-VII-1981, 2N, 6-X-1981, 2♂ 4♀, 26-VIII-1996, 49♂ 24♀, 13-VII-1997, 1♂; stream in Black Hills Experimental Forest, 14-VI to 26-VIII-1995, 1♀ (SDSU), 24-VIII-1996, 9♀ (SDSU). *Pennington Co.:* Beaver Creek, 23-VIII-1996, 1♂ 2♀, 16-VII-1997, 8♂ 2♀; Burnt Fork, 23-VIII-1996, 4♂ 10♀; Castle Creek, 23-VIII-1996, 19♂ 6♀; Deer Creek, 24-VIII-1996, 1♂ 1♀; Ditch Creek, 23-VIII-1996, 2♂; Newton Fork, 23-VIII-1996, 3♂ 6♀; North Fork Castle Creek, 24-VIII-1996, 7♂ 10♀; Palmer Creek, 23-VIII-1996, 1♂; Pine Creek, 22-VIII-1996, 1♂ 1♀; Rapid Creek, 24-VIII-1996, 1♂ 1♀; Spring Creek, 21-VIII-1996, 10♂ 3♀; creek in Sunday Gulch, 21-VIII-1996, 5♂ 2♀; stream in Jenny Gulch, 11-VII-1997, 35♂ 8♀; Willow Creek, 23-VIII-1996, 1♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Beaver Creek, 27-VIII-1996, 2♂ 1♀; Blacktail Creek, 27-VIII-1996, 6♂ 4♀, 16-VII-1997, 1♂; Cold Springs Creek, 28-VIII-1996, 13♂ 14♀, 16-VII-1997, 6♂ 9♀; Lytle Creek, 27-VIII-1996, 28♂ 6♀; Whitelaw Creek, 27-VIII-1996, 3♂. *Weston Co.:* Cold Creek, 16-VII-1997, 9♂ 14♀.

DISCUSSION.—This species occurs throughout the southern and central Rockies (Baumann et al. 1977). The Black Hills population represents the easternmost range limit for this species.

Genus *Malenka*
Malenka coloradensis (Banks)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Custer [probably French Creek], 13-VIII-1937, 1♂ (SDSU); stream entering Sylvan Lake, 5-VI-1995, 28♂ 17♀ 30N, 9-VII-1997, 3♂ 6♀. *Lawrence Co.:* Iron Creek, 7-VI-1995, 1♂, 13-VII-1997, 1♀; Little Spearfish Creek, 21-V-1981, 3♂; South Fork Rapid Creek, 12-VII-1997, 1♂; Spearfish Creek, 20-V-1981, 7N, 9-XII-1981, 4N, 7-VI-1995, 16♂ 3♀, 13-VII-1997, 1♀; tributary of Bear Butte Creek, 22-IV-1996, 4N, 12-VII-1997, 3♂ 7♀; tributary of Whitewood Creek, 12-VII-1997, 1♂ 2♀; Whitewood Creek, 7-VI-1995, 8♂ 5♀. *Pennington Co.:* Elkhorn Spring, 5-VI-1995, 14♂ 23♀, 22-VIII-1996, 3♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Blacktail Creek, 16-VII-1997, 1♂ 1♀.

DISCUSSION.—This species is most common in the southern portion of the Rocky Mountains (Baumann et al. 1977). The Black Hills population represents the northeast range limit for this species. In the Black Hills *M. coloradensis* was collected in habitats ranging from small springs to larger creeks.

Genus *Nemoura*

Nemoura trispinosa Claassen

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Sylvan Lake, 15-VI-1953, 1♀ (USNM). *Lawrence Co.:* Englewood (probably Whitewood Creek), 17-VI-1936, 1♀ (SDSU); Spearfish Creek, 28-VI-1965, 2♀ (USNM), 27-VI-1995, 52♂ 21♀; stream in Black Hills Experimental Forest, 14-VI to 26-VIII-1995, 25♂ 18♀ (SDSU); tributary of Bear Butte Creek, 12-VII-1997, 1♂ 1♀; tributary of Whitewood Creek, 12-VII-1997, 1♀; Whitewood Creek, 17-VI-1936, 1♀, 7-VI-1995, 1♂ 1♀. *Pennington Co.:* Burnt Fork, 6-VI-1995, 13♂ 26♀, 11-VII-1997, 4♂ 9♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Blacktail Creek, 16-VII-1997, 4♂ 7♀; Whitelaw Creek, 16-VII-1997, 1♂.

DISCUSSION.—This species is known from Labrador west to Manitoba and south to Illinois (Stark et al. 1986). The Black Hills represent the westernmost range limit for this species. In the Black Hills *N. trispinosa* was associated with spring-influenced systems.

Genus *Prostoia*

Prostoia besametsa (Ricker)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Custer State Park, 17-VI-1955, 1♂ (SDSU); Iron Creek, 20-IV-1996, 10♂ 8♀ 12N, 10-VII-1997, 1♀. *Lawrence Co.:* Boxelder Creek, 22-IV-1996, 1♀ 2N; East Spearfish Creek, 20-V-1981, 1♀, 7-VI-1995, 4♀, 23-IV-1996, 3♂ 6N; Hay Creek, 22-IV-1996, 1♂ 1N; Iron Creek, 23-IV-1996, 18♂ 6♀; Little Spearfish Creek, 17-III-1981, 19N, 21-V-1981, 4♂ 6♀, 27-IV-1995, 3♀ (SDSU), 23-IV-1996, 3♂ 1♀; South Fork Boxelder Creek, 22-IV-1996, 3♂ 6N; South Fork Rapid Creek, 22-V-1981, 2♀; Spearfish Creek, 25-III-1968, 1N (INHS), 19-III-1981, 47N, 20-V-1981, 1♂ 4♀, 25-III-1982, 1N, 7-II-1995, 2N, 23-IV-1996, 13♂ 7♀, 13-VII-1997, 1♀; tributary of Bear Butte Creek, 22-IV-1996, 9N; Whitetail Creek, 19-III-1981, 2N; Whitewood Creek, 18-III-1981, 3N, 20-V-1981, 1♂ 14♀, 25-III-1982, 4N. *Pennington Co.:* Battle Creek, 5-II-1995, 10N; Beaver Creek, 16-VII-1997, 1♀; Grizzly Bear Creek, 20-IV-1996, 10N; creek in Sunday Gulch, 5-VI-1995, 1♂ 6♀, 9-VII-1997, 1♂ 1♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Beaver Creek, 24-IV-1996, 10♂ 1♀; North Redwater Creek, 24-IV-1996, 3N; Whitelaw Creek, 16-VII-1997, 3♀. *Weston Co.:* Beaver Creek, 23-IV-1996, 6N.

DISCUSSION.—This species occurs throughout the Rocky, Cascade, Coast, and Sierra Nevada Mountains (Baumann et al. 1977). The Black Hills population represents the easternmost range limit for this species.

Genus *Zapada*

Zapada cinctipes (Banks)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Iron Creek, 20-IV-1996, 22♂ 19♀; stream entering Sylvan Lake, 5-VI-1995, 1♀, 9-VII-1997, 1♀; stream 10 mi S of Sylvan Lake on Needles Hwy, 25-III-1968, 1♂ 1♀ (INHS); Willow Creek, 19-IV-1996, 4♂ 4♀, 4-VI-1995, 1♀. *Lawrence Co.:* Bear Butte Creek, 22-IV-1996, 4♂ 3♀; Boxelder Creek, 24-III-1968, 1♂ (INHS), 6-II-1995, 2N, 22-IV-1996, 3♂ 3♀; East Spearfish Creek, 20-V-1981, 15♂ 14♀ 1N, 7-II-1995, 12N, 7-VI-1995, 19♂ 14♀, 23-IV-1996, 13♂ 13♀, 25-VIII-1996, 5N; Elk Creek, 25-III-1968, 1♀ (INHS), 22-IV-1996, 9♂ 3♀, 25-VIII-1996, 4N; Estes Creek, 24-III-1968, 24♂ 9♀ (INHS); False Bottom Creek, 24-III-1968, 2♂ (INHS); Hay Creek, 22-IV-1996, 1♂ 1N, 25-VIII-1996, 5N; Iron Creek, 7-II-1995, 5♂* 7♀* 20N, 7-VI-1995, 3♂ 1♀, 23-IV-1996, 14♂ 9♀, 26-VIII-1996, 2N; Jim Creek, 6-II-1995, 2♂* 1♀*; Little Elk Creek, 22-IV-1996, 2♀; Little Spearfish Creek, 17-III-1981, 15♂ 21♀ 20N, 21-V-1981, 7♀ (INHS), 15-X-1994, 1N (SDSU), 27-IV-1995, 3♂ 5♀, 7-VI-1995, 2♀, 23-IV-1996, 10♂ 11♀, 26-VIII-1996, 2N, 13-VII-1997, 1♀; North Boxelder Creek, 22-IV-1996, 2♂ 1♀; creek SE of Pluma [probably West Strawberry Creek], 24-III-1968, 1♀ 1N (INHS); South Fork Boxelder Creek, 22-IV-1996, 10♂ 10♀; South Fork Rapid Creek, 22-V-1981, 1♂ 1♀; Spearfish Creek, 27-VII-1940, 2N (INHS), 25-III-1968, 27♂ 36♀ (INHS), 19-III-1981, 7♂ 1♀ 70N, 20-V-1981, 5♂ 16♀, 6-X-1981, 20N, 9-XII-1981, 20N, 25-III-1982, 53♂ 40♀, 7-II-1995, 25N, 7-VI-1995, 14♂ 17♀, 23-IV-1996, 54♂ 48♀, 26-VIII-1996, 13N, 13-VII-1997, 1♀; Strawberry Creek [probably West Strawberry Creek], 10-XII-1981, 20N, 23-III-1982, 1♀ 3N; tributary of Bear Butte Creek, 22-IV-1996, 9♂ 11♀, 24-VIII-1996, 4N; Whitetail Creek, 19-III-1981, 3♂ 5♀ 20N, 20-V-1981, 1♂ 12♀, 16-VII-1981, 1N, 8-X-1981, 8N, 9-XII-1981, 3N; Whitewood Creek, 18-III-1981, 14♂ 7♀ 26N, 20-V-1981, 5♂ 102♀, 15-

VII-1981, 9N, 7-X-1981, 37N, 9-XII-1981, 31N, 25-III-1982, 18♂ 23♀ 35N, 7-II-1995, 4N. *Meade Co.:* Elk Creek, 22-IV-1996, 2♀; Meadow Creek, 22-IV-1996, 15♂ 7♀. *Pennington Co.:* Battle Creek, 8-II-1995, 1♂* 5N; Beaver Creek, 23-VIII-1996, 7N; Burnt Fork, 6-VI-1995, 4♀, 21-IV-1996, 11♂ 7♀; Castle Creek, 9-II-1995, 19N, 21-IV-1996, 24♂ 13♀; Deer Creek, 21-IV-1996, 1♂ 1♀; Ditch Creek, 23-VIII-1996, 1N; Grizzly Bear Creek, 20-IV-1996, 2♀; Middle Fork Boxelder Creek, 6-VI-1995, 2♀, 22-IV-1996, 15♂ 10♀; Newton Fork, 9-II-1995, 6N, 6-VI-1995, 1♀, 21-IV-1996, 5♂ 3♀; North Fork Castle Creek, 21-IV-1996, 2♂, 24-VIII-1996, 1N; Palmer Creek, 8-II-1995, 7N, 20-IV-1996, 1♂ 8♀; Pine Creek, 20-IV-1996, 2♂ 1♀; Rapid Creek, 24-III-1968, 24♂ 15♀, 6-II-1995, 2♂* 13N, 6-VI-1995, 1♂ 2♀, 21-IV-1996, 6♂ 6♀; Slate Creek, 21-IV-1996, 9♂ 10♀; South Fork Castle Creek, 21-IV-1996, 14♂ 7♀; Spokane Creek, 20-IV-1996, 1♂ 6♀; Spring Creek, 19-III-1988, 1♂ 2♀, 19-IV-1996, 1♂ 2♀; creek in Sunday Gulch, 8-II-1995, 4N, 5-VI-1995, 5♀, 19-IV-1996, 11♂ 13♀; Willow Creek, 20-IV-1996, 3♀.

Wyoming distribution.—*Crook Co.:* Beaver Creek, 24-IV-1996, 4♂ 6♀, 27-VIII-1996, 1N; Lytle Creek, 27-VIII-1996, 5N; North Redwater Creek, 24-IV-1996, 2♀, 27-VIII-1996, 7N. *Weston Co.:* Beaver Creek, 23-IV-1996, 7♂ 7♀; Cold Creek, 23-IV-1996, 10♂ 14♀.

Discussion.—This species is perhaps the most common and vagile species of the Euholognatha in western North America. It is found throughout the Rocky, Cascade, Coast, and Sierra Nevada Mountains (Baumann et al. 1977). It is also one of the most common stonefly species in the Black Hills, occurring in both small and large streams.

Family Capniidae

Genus *Capnia*

Capnia confusa Claassen

South Dakota distribution.—*Custer Co.:* Grace Coolidge Creek, 5-VI-1995, 2♀; Iron Creek, 5-VI-1995, 2♀, 20-IV-1996, 11♂ 4♀. *Lawrence Co.:* East Spearfish Creek, 7-VI-1995, 4♀, 23-IV-1996, 1♂; Iron Creek, 7-VI-1995, 1♀, 23-IV-1996, 2♂ 1♀; Little Spearfish Creek, 23-IV-1996, 1♂; Spearfish Creek, 25-III-1968, 4♂ (INHS), 7-VI-1995, 4♀, 23-IV-1996, 35♂ 26♀; Whitewood Creek, 20-V-1981, 2♀. *Pennington Co.:* Deer Creek, 21-IV-1996, 1♂ 1♀; Rapid Creek, 6-VI-1995, 1♂ 2♀, 21-IV-1996, 56♂ 18♀; South Fork Castle Creek, 21-IV-1996, 4♂; creek in Sunday Gulch, 5-VI-1995, 3♀, 19-IV-1996, 5♂ 6♀.

Discussion.—This species is widespread and common throughout the West, occurring from Alaska south to New Mexico and east to Manitoba (Nelson and Baumann 1989).

Capnia gracilaria Claassen

South Dakota distribution.—*Custer Co.:* Iron Creek, 20-IV-1996, 2♂ 6♀; Willow Creek, 19-IV-1996, 3♂ 1♀. *Lawrence Co.:* East Spearfish Creek, 20-V-1981, 1♀, 7-VI-1995, 1♀, 23-IV-1996, 2♂ 1♀; Elk Creek, 25-III-1968, 1♀ (INHS); Iron Creek, 7-II-1995, 2♂*, 23-IV-1996, 20♂ 10♀; Little Spearfish Creek, 17-III-1981, 1♀, 23-IV-1996, 7♂ 1♀; Spearfish Creek, 25-III-1968, 30♂ 20♀ (INHS), 19-III-1981, 7♂ 1♀, 20-V-1981, 8♀, 25-III-1982, 40♂ 9N, 7-VI-1995, 4♀, 23-IV-1996, 19♂ 6♀; tributary of Bear Butte Creek, 22-IV-1996, 22♂ 21♀. *Pennington Co.:* Burnt Fork, 21-IV-1996, 22♂ 26♀; Deer Creek, 21-IV-1996, 3♀; Elkhorn Spring, 5-VI-1995, 1♂ 12♀, 20-IV-1996, 44♂ 35♀; Pine Creek, 5-VI-1995, 1♀, 20-IV-1996, 6♂ 7♀; Spokane Creek, 20-IV-1996, 2♂ 1♀; creek in Sunday Gulch, 19-IV-1996, 3♀; Willow Creek, 5-VI-1995, 1♀, 20-IV-1996, 9♂ 5♀.

Discussion.—This widespread species is very common throughout western North America, occurring from Alaska south to Baja California and east to Manitoba (Nelson and Baumann 1989). The Black Hills represent the northeastern limit for *C. gracilaria*.

Genus *Eucapnopsis*

Eucapnopsis brevicauda Claassen

South Dakota distribution.—*Custer Co.:* Iron Creek, 5-VI-1995, 2♀, 20-IV-1996, 17♂ 9♀. *Lawrence Co.:* Iron Creek, 23-IV-1996, 1♀; Spearfish Creek, 23-IV-1996, 22♂ 17♀; Whitewood Creek, 20-V-1981, 1♀. *Pennington Co.:* Pine Creek, 5-VI-1995, 2♀; Rapid Creek, 21-IV-1996, 2♂ 6♀; creek in Sunday Gulch, 5-VI-1995, 1♂ 1♀, 9-VII-1997, 2♀; Willow Creek, 5-VI-1995, 1♀.

Discussion.—This late-emerging winter stonefly is found throughout the Rocky, Cascade, Coast, and Sierra Nevada Mountains.

Genus *Isocapnia*

Isocapnia sp. A

South Dakota distribution.—*Lawrence Co.:* Spearfish Creek, near jct Redwater River, 24-III-1982, 1♀.

Discussion.—The genus *Isocapnia* is interesting because of its rarity. The specimen collected in the Black Hills is of special interest because of the brachyptery of the female, a condition unreported for the genus. Males are required for specific determination.

Genus *Paracapnia*

Paracapnia angulata Hanson

South Dakota distribution.—*Lawrence Co.:* Bear Butte Creek, 22-IV-1996, 1♂ 6♀; Boxelder

Creek, 24-III-1968, 2♂ (INHS), 22-IV-1996, 1♀; Hay Creek, 22-IV-1996, 1♀; Iron Creek, 7-II-1995, 1♂* 6♀*; Jim Creek, 6-II-1995, 3N; Little Elk Creek, 22-IV-1996, 1♂ 4♀. *Meade Co.:* Elk Creek, 22-IV-1996, 10♂ 18♀. *Pennington Co.:* Battle Creek, 8-II-1995, 1♀*; Boxelder Creek, 22-IV-1996, 14♂ 23♀; Burnt Fork, 21-IV-1996, 9♂ 3♀; Grizzly Bear Creek, 20-IV-1996, 1♂; Horse Creek, 18-III-1988, 11♂ 13♀; Middle Fork Boxelder Creek, 22-IV-1996, 1♀; Palmer Creek, 5-VI-1995, 1♀, 20-IV-1996, 2♂ 1♀; Rapid Creek, 21-IV-1996, 2♂ 1♀; Spring Creek, 19-III-1988, 8♀; creek in Sunday Gulch, 5-VI-1995, 4♀, 19-IV-1996, 6♂ 5♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Beaver Creek, 24-IV-1996, 27♂ 44♀.

DISCUSSION.—This eastern North American species has a remarkable geographic distribution. It occurs primarily from Quebec south to Tennessee; however, there are isolated populations reported in the Ozarks of Oklahoma, Rockies of Colorado and Wyoming, boreal streams of Manitoba and Saskatchewan, and now in the Black Hills.

Genus *Utacapnia*

Utacapnia lemoniana (Nebeker and Gaufin)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Willow Creek, Hwy 89, N of Custer, 4-VI-1995, 1♀, 19-IV-1996, 3♂ 7♀. *Lawrence Co.:* tributary of Bear Butte Creek, Strawberry Picnic Area, 22-IV-1996, 1♂. *Pennington Co.:* Burnt Fork, rd 389, NW of Hill City, 6-VI-1995, 1♀, 21-IV-1996, 3♂ 5♀; North Fork Castle Creek, rd 306, Mercedes Gulch, 21-IV-1996, 1♂ 1♀.

DISCUSSION.—This species occurs in the central Rocky Mountains. The Black Hills populations represent the easternmost range limit for this species.

Family Leuctridae

Genus *Paraleuctra*

Paraleuctra vershina Gaufin and Ricker

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Grace Coolidge Creek, 5-VI-1995, 14♂ 12♀; Iron Creek, 5-VI-1995, 24♂ 12♀, 10-VII-1997, 7♂ 6♀. *Meade Co.:* Sturgis [probably Bear Butte Creek], 26-V-1951, 1♀ (SDSU). *Lawrence Co.:* East Spearfish Creek, 17-VI-1936, 1♀ (SDSU); Iron Creek, 7-VI-1995, 2♂ 6♀; Lead Creek [probably Whitewood Creek], 9-VI-1973, 5♂ 4♀; Spearfish Creek, 20-V-1981, 1♂, 7-VI-1995, 13♂ 18♀, 13-VII-1997, 1♀; Whitetail Creek, 20-V-1981, 1♂; Whitewood Creek, 25-III-1982, 1N. *Pennington Co.:* Elkhorn Spring, 5-VI-1995, 65♂ 31♀; Grizzly Bear Creek, 10-VII-1997, 2♀; Horse Creek, 6-VI-1995, 1♀; Palmer Creek, 5-VI-1995, 1♂, 10-VII-1997, 2♀; Pine Creek, 5-VI-1995, 45♂ 17♀, 10-VII-1997, 1♀; creek in Sunday Gulch, 5-VI-1995, 8♂ 1♀, 9-VII-1997, 1♂ 2♀; Willow Creek, 5-VI-1995, 24♂ 9♀, 10-VII-1997, 7♂ 19♀.

DISCUSSION.—This species is the only leuctrid found in the Black Hills. *Paraleuctra vershina* is found throughout the West, including the Coast, Cascade, Rocky, and Sierra Nevada Mountains. The Black Hills population represents the easternmost range limit for this species.

Group Systellognatha
Family Perlodidae

Genus *Isogenoides*

Isogenoides elongatus (Hagen)

SOUTH DAKOTA DISTRIBUTION.—*Lawrence Co.:* Spearfish Creek, Hwy 85, above Cheyenne Crossing, 7-II-1995, 3♀*. *Pennington Co.:* Rapid Creek, 6-II-1995, 1♂* 10N, 6-VI-1995, 9♂ 3♀, 21-IV-1996, 9N.

DISCUSSION.—This species is typically found in larger creeks and rivers in the West. In the Black Hills, *I. elongatus* was collected in only 2 of the larger streams.

Genus *Isoperla*

Isoperla longiseta Banks

SOUTH DAKOTA DISTRIBUTION.—*Butte Co.:* Belle Fourche River, Belle Fourche, 7-VI-1995, 2♀; Newell [probably Belle Fourche River], 19-VII-1923, 1♂ (INHS). *Fall River Co.:* Oral [probably Cheyenne River], 4-VII-1953, 1♂ (INHS).

WYOMING DISTRIBUTION.—*Crook Co.:* Belle Fourche River, Hwy 24, Hulett, 15-VII-1997, 1♀.

DISCUSSION.—This species is one of the few species common in the prairies (Ricker 1946, 1964). It is found throughout the West and Midwest in larger rivers. In the Black Hills, *I. longiseta* is found in the 2 large rivers that drain the area.

Isoperla phalerata (Smith)

SOUTH DAKOTA DISTRIBUTION.—*Butte Co.:* Redwater River, 7-II-1995, 1N. *Custer Co.:* Beaver Creek, 11-VI-1975, 1♂ 2♀ (PURC), 9-VII-1997, 1♀; Grace Coolidge Creek, 10-VII-1997, 1♀; Iron Creek, 6-VII-1968, 1♂ 1♀, 5-VI-1995, 1♂, 20-IV-1996, 3N, 22-VIII-1996, 3N, 10-VII-1997, 4♀; Little Squaw Creek, 15-IX-1970, 1♂*, 10-VII-1997, 2♀. *Lawrence Co.:* Bear Butte Creek, 22-IV-1996, 3N; Black Hills Natl Forest near Savoy, [probably Spearfish Creek], 6-VII-1968, 1♀ (INHS); Boxelder Creek, 6-II-1995, 3N, 25-VIII-1996, 1N; Cold Springs Creek, 20-V-1981, 3N; East Spearfish Creek, 7-VI-1995, 1♂, 13-VII-1997, 1♀; Elk Creek, 22-IV-1996, 7N; Englewood [probably Whitewood Creek], 18-VI-1925, 1♂ (INHS); Little Spearfish Creek, 17-III-1981, 11N, 23-IV-1996, 3N, 13-VII-1997, 1♂ 1♀; South Fork Boxelder Creek, 22-IV-1996, 5N, 12-VII-1997, 1♀; South Fork Rapid Creek, 12-VII-1997, 1♂ 4♀; Spearfish Creek, 18-VI-1966, 1♂ (SDSU), 9-VI-1971, 3♀ (SDSU), 17-III-1981, 5N, 20-V-1981, 1♂ 3♀ 5N, 6-X-1981, 7N, 9-XII-1981, 17N, 25-III-1982, 19N, 7-II-1995, 4N, 7-VI-1995, 1♀, 13-VII-1997, 3♂ 2♀; Whitewood Creek, 19-V-1981, 1♂ 1N, 6-X-1981, 5N, 9-XII-1981, 5N, 25-III-1982, 6N. *Meade Co.:* Elk Creek, 22-IV-1996, 7N; Meadow Creek, 22-IV-1996, 5N. *Pennington Co.:* Battle Creek, 8-II-1995, 4♂* 2♀*; Beaver Creek, 16-VII-1997, 3♀; Boxelder Creek, 22-IV-1996, 3N; Castle Creek, 9-II-1995, 2N; Deer Creek, 21-IV-1996, 2♀* 4N, 24-VIII-1996, 1N; Grizzly Bear Creek, 20-IV-1996, 1N; Middle Fork Boxelder Creek, 6-VI-1995, 2♂* 4♀*, 22-IV-1996, 2N; Newton Fork, 23-VIII-1996, 3N, 11-VII-1997, 3♀, North Fork Castle Creek, 24-VIII-1996, 1N; Palmer Creek, 8-II-1995, 2N, 20-IV-1996, 2N, 10-VII-1997, 1♀; Rapid Creek, 6-II-1995, 6N, 6-VI-1995, 2N, 21-IV-1996, 4N, 11-VII-1997, 2E; Spring Creek, 19-III-1988, 8N, 6-VI-1995, 5♂ 5♀, 19-IV-1996, 3N, 21-VIII-1996, 4N; creek in Sunday Gulch, 5-VI-1995, 1♂* 1♀*, 19-IV-1996, 1N; stream in Jenny Gulch, 11-VII-1997, 1♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Beaver Creek, 24-IV-1996, 6N; Cold Springs Creek, 28-VIII-1996, 10N; Redwater Creek, 19-III-1981, 20N; Sand Creek, 19-III-1981, 60N, 21-V-1981, 3♂ 5♀ 15N, 7-X-1981, 12N, 8-XII-1981, 40N, 24-III-1982, 12N, 24-IV-1996, 7♂ 2♀. *Weston Co.:* Cold Creek, 23-IV-1996, 4N, 16-VII-1997, 2♂ 4♀.

DISCUSSION.—The distribution of this species is interesting in that it is considered uncommon throughout the West (Szczytko and Stewart 1979) but is common in the Black Hills. This may be due to a lack of competition from other medium-sized predatory stoneflies.

Isoperla quinquepunctata (Banks)

SOUTH DAKOTA DISTRIBUTION.—*Butte Co.:* Belle Fourche River, 7-VI-1995, 1♀; Redwater River, 7-II-1995, 13N. *Custer Co.:* Battle Creek, 5-II-1995, 8N; Beaver Creek, 9-VII-1997, 14♂ 10♀; Flynn Creek, 9-VII-1997, 2♂; French Creek, 9-VII-1997, 4♀; Grace Coolidge Creek, 5-II-1995, 3N, 10-VII-1997, 8♂ 12♀; Little Squaw Creek, 10-VII-1997, 8♂ 3♀; Iron Creek, 5-VI-1995, 1N, 10-VII-1997, 11♂ 18♀; Spokane Creek, 10-VII-1997, 4♂ 13♀; tributary of Beaver Creek, 9-VII-1997, 1♂ 3♀. *Lawrence Co.:* Boxelder Creek, 13-VI-1975, 1N, 6-II-1995, 16N, 22-IV-1996, 2N, 12-VII-1997, 31♂ 26♀; Hay Creek, 22-IV-1996, 1N; Jim Creek, 11-VII-1997, 14♂ 18♀; Little Elk Creek, 22-IV-1996, 12N, 25-VIII-1996, 1♂ 3♀, 12-VII-1997, 7♂ 5♀; Little Spearfish Creek, 17-III-1981, 2N, 7-VI-1995, 1N, 23-IV-1996, 2N, 13-VII-1997, 8♂ 2♀; Redwater River, 13-VII-1997, 66♂ 20♀; South Fork Boxelder Creek, 12-VII-1997, 28♂ 19♀; Spearfish Creek, 27-VII-1940, 27♂ 13♀ 19N (INHS), 1-VI-1961, 1♀ (NDSU), 9-VI-1971, 3♂ (SDSU), 21-V-1981, 83♂ 27♀, 16-VII-1981, 1♂, 24-III-1982, 30N, 7-II-1995, 10N, 7-VI-1995, 1N, 13-VII-1997, 16♂ 14♀; Strawberry Creek [probably West Strawberry Creek], 23-III-1982, 3N; tributary of Bear Butte Creek, 12-VII-1997, 1♀; Whitewood Creek, 19-V-1981, 1N, 23-III-1982, 3N, 14-VI-1982, 5N. *Meade Co.:* Elk Creek, 22-IV-1996, 13N; Meadow Creek, 22-IV-1996, 1N. *Pennington Co.:* Battle Creek, 8-II-1995, 1♂; Beaver Creek, 16-VII-1997, 2♂; Boxelder Creek, 22-IV-1996, 3N; Deer Creek, 21-IV-1996, 1N, 11-VII-1997, 46♂ 49♀; Grizzly Bear Creek, 10-VII-1997, 2♂ 1♀; Newton Fork, 11-VII-1997, 26♂ 10♀; North Fork Castle Creek, 18-VIII-1954, 1♀ (INHS); Palmer Creek, 10-VII-1997, 1♀; Rapid Creek, 6-II-1995, 1N, 6-VI-1995, 2♂ 2♀* 9N, 21-IV-1996, 4N, 24-VIII-1996, 1♀ 18N, 11-VII-1997, 15♂ 24♀; Spring Creek, 19-III-1988, 1N, 19-IV-1996, 14N, 21-VIII-1996, 4♂ 1♀, 11-VII-1997, 31♂ 19♀; creek in Sunday Gulch, 5-VI-1995, 1N; stream in Jenny Gulch, 11-VII-1997, 1♂ 1♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Beaver Creek, 24-IV-1996, 7N, 16-VII-1997, 5♂ 1♀; Beaver Creek, 8-VI-1995, 7♂ 7♀; Cold Springs Creek, 16-VII-1997, 3♂ 1♀; Lame Jones Creek, 16-VII-1997, 14♂ 21♀; North Redwater Creek, 24-IV-1996, 6N; Redwater Creek, 19-III-1981, 30N; Sand Creek, 19-III-1981, 50N, 21-V-1981, 35♂ 14♀ 3N, 16-VII-1981, 1♂ 8N, 8-XII-1981, 20N, 24-III-1982, 25N, 24-IV-1996, 15N, 28-VIII-1996, 7♂ 14♀; Whitelaw Creek, 16-VII-1997, 17♂ 24♀. *Weston Co.:* Cold Creek, 16-VII-1997, 3♂ 2♀.

DISCUSSION.—This widespread western North American species is common throughout the Black Hills. Szczytko and Stewart (1978) synonymized *I. patricia* Frison, originally described from Spearfish, South Dakota, with *I. quinquepunctata.*

Isoperla transmarina (Newman)

SOUTH DAKOTA DISTRIBUTION.—*Pennington Co.:* Rapid Creek, Pactola Inlet, Silver City, 6-II-1995, 1♂, 6-VI-1995, 3♂ 1♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Beaver Creek, above Cook Lake, Cook Lake Campground, 16-VII-1997, 1♀.

DISCUSSION.—This species is found in the northeastern United States and across Canada (Stark et al. 1986). The Black Hills population represents a southwest range extension for this species.

Genus *Skwala*

Skwala americana (Klapalek)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Iron Creek, 20-IV-1996, 3♂ 12N, 22-VIII-1996, 11N. *Lawrence Co.:* Boxelder Creek, 6-II-1995, 10N, 22-IV-1996, 1N, 25-VIII-1996, 10N; Elk Creek, 22-IV-1996, 1♀ 6N; Iron Creek, 23-IV-1996, 1♀; North Boxelder Creek, 22-IV-1996, 2N; South Fork Boxelder Creek, 25-VIII-1996, 1N; Spearfish Creek, 27-VII-1940, 3E (INHS), 17-III-1981, 2N, 21-V-1981, 1E, 16-VII-1981, 1N, 23-IX-1995, 20N (SDSU), 23-IV-1996, 9♂ 11♀, 26-VIII-1996, 19N; Strawberry Creek [probably West Strawberry Creek], 10-XII-1981, 6N; tributary of Elk Creek, 24-III-1968, 1N (INHS); Whitetail Creek, 9-XII-1981, 1N; Whitewood Creek, 18-III-1981, 5N, 8-X-1981, 2N, 9-XII-1981, 2N, 25-III-1982, 1N, 7-II-1995, 7N. *Pennington Co.:* Battle Creek, 8-II-1995, 5♂* 2N; Boxelder Creek, 22-IV-1996, 1N; Burnt Fork, 21-IV-1996, 1♀, 23-VIII-1996, 1N; Castle Creek, 9-II-1995, 7N; Grizzly Bear Creek, 20-IV-1996, 9♂, 22-VIII-1996, 8N; Horse Creek, 18-III-1988, 4N; North Fork Castle Creek, 24-VIII-1996, 1N; Rapid Creek, 6-II-1995, 1♂*; Spring Creek, 9-II-1995, 8N, 19-IV-1996, 1♂* 5♀* 1♂ 17N, 21-VIII-1996, 4N; creek in Sunday Gulch, 5-VI-1995, 1N, 19-IV-1996, 14♂ 3N.

Wyoming distribution.—*Crook Co.:* Beaver Creek, 27-VIII-1996, 2N; Whitelaw Creek, 27-VIII-1996, 3N.

Discussion.—A widespread species of the Rocky, Cascade, Coast, and Sierra Nevada Mountains (Baumann et al. 1977), *S. americana* is the common large predatory stonefly in the Black Hills. This species was previously known as *S. parallela* (Frison).

Family Perlidae

Genus *Acroneuria*

Acroneuria abnormis (Newman)

South Dakota distribution.—*Butte Co.:* Belle Fourche River, Belle Fourche, 23-IV-1996, 4N.

Wyoming distribution.—*Crook Co.:* Belle Fourche River, Hwy 24, Hulett, 7-II-1995, 1N.

Discussion.—This is one of the most widespread species in all of North America (Stark et al. 1986). It is generally found in larger streams. It was not found in the Black Hills proper but was found in the Belle Fourche River, which drains the northern section of the Black Hills and the Bear Lodge Mountains.

Genus *Claassenia*

Claassenia sabulosa (Banks)

South Dakota distribution.—*Lawrence Co.:* Boxelder Creek, Boxelder Forks Campground, 13-VI-1975, 1N (PURC), 6-II-1995, 1N, 12-VII-1997, 1♂; Spearfish, 25-VII-1924, 1♂ (INHS), 27-VII-1940, 3E (INHS); Spearfish Creek, Hwy 14A, Botany Bay Picnic Area, 26-VIII-1996, 1N; Whitewood Creek, near confluence Whitetail Creek, 19-III-1981, 4N, 7-X-1981, 2N, 25-III-1982, 1N; Rapid Creek, Hwy 44, near Big Bend, 6-II-1995, 9N; Rapid Creek, Pactola Inlet, Silver City, 6-VI-1995, 2N, 21-IV-1996, 1N, 24-VIII-1996, 7N.

Discussion.—This large, active perlid is common throughout the West in larger streams, but it also has a disjunct population in Quebec (Stark et al. 1986). Its distribution in the Black Hills is limited.

Genus *Hesperoperla*

Hesperoperla pacifica (Banks)

South Dakota distribution.—*Custer Co.:* Iron Creek, 5-VI-1995, 6N, 20-IV-1996, 9N, 22-VIII-1996, 4N; Little Squaw Creek, 15-IX-1970, 1N, 10-VII-1997, 3♂ 3♀. *Lawrence Co.:* Boxelder Creek, 13-VI-1975, 1♂ 3N (PURC), 6-II-1995, 3N, 22-IV-1996, 1N, 25-VIII-1996, 3N; East Spearfish Creek, 20-V-1981, 1N, 7-II-1995, 4N, 7-VI-1995, 3N, 25-VIII-1996, 1N; Elk Creek, 25-VIII-1996, 6N; Hay Creek, 22-IV-1996, 2N; Iron Creek, 7-II-1995, 5N, 7-VI-1995, 3♂ 2♀ 5N, 23-IV-1996, 4N, 26-VIII-1996, 3N, 13-VII-1997, 2♂ 2♀; Jim Creek, 13-VI-1975, 7N (PURC), 6-II-1995, 1N; Little Elk Creek, 25-VIII-1996, 3N; Little Spearfish Creek, 17-III-1981, 3N, 21-V-1981, 1N, 15-X-1994, 9N (SDSU), 23-IV-1996, 3N, 7-VI-1995, 3N, 26-VIII-1996, 4N, 13-VII-1997, 3♂ 2♀; South Fork Boxelder Creek, 22-IV-1996, 2N, 12-VII-1997, 1♂ 2♀; South Fork Rapid Creek, 4-VIII-1967, 1♂ 1♀ (SDSU); Spearfish Creek, 27-VII-1940, 32N (INHS), 19-III-1981, 8N, 20-V-1981, 7N, 16-VII-1981, 7N, 6-X-1981, 5N, 9-XII-1981, 8N, 25-III-1982, 15N, 7-II-1995, 12N, 7-VI-1995, 2N, 23-IV-1996, 2N, 26-VIII-1996, 9N; Strawberry Creek [probably West Strawberry Creek], 10-XII-1981, 2N, 23-III-1982, 3N; tributary of Bear Butte Creek, 22-IV-1996, 6N, 24-VIII-1996, 5N, 12-VII-1997, 1♂; tributary of Whitewood Creek, 12-VII-1997, 1♂; Whitetail Creek, 19-III-1981, 4N, 16-VII-1981, 2N, 8-X-1981, 1N, 9-XII-1981, 1N; Whitewood Creek, 19-III-1981, 50N, 19-V-1981, 1♂ 2 ♀ 24N, 15-VII-1981, 27N, 7-X-1981, 21N, 8-XII-1981, 26N, 23-III-1982, 13N, 14-VI-1982, 9N, 7-VI-1995, 4N. *Pennington Co.*: Battle Creek, 8-II-1995, 1N; Beaver Creek, 23-VIII-1996, 2N, 16-VII-1997, 2♀; Castle Creek, 9-II-1995, 8N, 23-VIII-1996, 3N; Ditch Creek, 23-VIII-1996, 4N; Grizzly Bear Creek, 5-VI-1995, 1N, 20-IV-1996, 8N, 22-VIII-1996, 3N, 10-VII-1997, 1♀; Newton Fork, 9-II-1995, 8N, 6-VI-1995, 7N, 21-IV-1996, 4N, 11-VII-1997, 2♀; Rapid Creek, 13-VI-1975, 1N (PURC), 6-II-1995, 6N, 21-IV-1996, 2N, 24-VIII-1996, 4N; Slate Creek, 21-IV-1996, 2N; South Fork Castle Creek, 21-IV-1996, 3N; creek in Sunday Gulch, 8-II-1995, 6N, 5-VI-1995, 2N, 19-IV-1996, 3N, 21-VIII-1996, 3N, 9-VII-1997, 1♂.

Wyoming distribution.—*Crook Co.:* Beaver Creek, 27-VIII-1996, 4N; Lytle Creek, 27-VIII-1996, 1N; Sand Creek, 19-III-1981, 19N, 21-V-1981, 1♂, 24-IV-1996, 1N, 28-VIII-1996, 2N; Whitelaw Creek, 27-VIII-1996, 2N. *Weston Co.:* Beaver Creek, 23-IV-1996, 3N; Cold Springs Creek, 27-V-1959, 1N (NDSU).

Discussion.—A typical western North American species, it occurs from Alaska south to New Mexico (Stark et al. 1986). It is also one of the most common species in the Black Hills, found in very small to very large streams. The Black Hills represent the easternmost range limit for this species.

Genus *Perlesta*
Perlesta decipiens (Walsh)

SOUTH DAKOTA DISTRIBUTION.—*Butte Co.:* Belle Fourche River, Belle Fourche, 13-VII-1997, 2♀. *Fall River Co.:* Cheyenne River, Angostura Reservoir, Angostura State Park, 8-VII-1997, 1♂ 2♀; Cheyenne River, Oral, below Angostura Reservoir, 8-VII-1997, 15♂ 9♀.

DISCUSSION.—*Perlesta decipiens* has a widespread distribution, ranging from Virginia to Colorado and from Wisconsin to Texas (Stark 1989). In the Black Hills, it was found in the 2 large rivers that drain the area but not in the Black Hills proper.

Family Chloroperlidae

Genus *Paraperla*
Paraperla frontalis (Banks)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Grace Coolidge Creek, 5-VI-1995, 1♂; Iron Creek, 5-VI-1995, 3♂ 2♀. *Lawrence Co.:* Black Hills National Forest near Savoy [probably Spearfish Creek], 6-VII-1968, 1♀ (INHS); East Spearfish Creek, 7-VI-1995, 2♂; Spearfish Creek, 21-V-1981, 1♀, 7-VI-1995, 3♀; Whitewood Creek, 18-III-1981, 6N, 19-V-1981, 2N. *Pennington Co.:* creek in Sunday Gulch, 5-VI-1995, 2♂ 1♀; Grizzly Bear Creek, 5-VI-1995, 1♂; Pine Creek, 5-VI-1995, 13♂ 2♀, 10-VII-1997, 1♀; Rapid Creek, 6-VI-1995, 2♂.

DISCUSSION.—Although this species is not common, it occurs in the Coast, Cascade, Sierra Nevada, and Rocky Mountains (Baumann et al. 1977). The Black Hills represent the easternmost range limit for this species.

Genus *Suwallia*
Suwallia lineosa (Banks)

SOUTH DAKOTA DISTRIBUTION.—*Lawrence Co.:* Little Spearfish Creek, Timon Campground, 13-VII-1997, 1♀; Spearfish Creek, Hwy 14A, Botany Bay Picnic Area, 13-VII-1997, 21♀; Spearfish Creek, Spearfish Water Diversion, Hwy 14A, 13-VII-1997, 2♀.

DISCUSSION.—This species is found in the Coast, Cascade, and Rocky Mountains (Baumann et al. 1977). The Black Hills population represents the easternmost range limit for this species.

Genus *Sweltsa*
Sweltsa borealis (Banks)

SOUTH DAKOTA DISTRIBUTION.—*Lawrence Co.:* Iron Creek, Hwy 14A, confl Spearfish Creek, 7-VI-1995, 1♂ 1♀; Spearfish Creek, Hwy 14A, below Bridal Veil Falls, 7-VI-1995, 1♀; Spearfish Creek, Hwy 85, above Cheyenne Crossing, 7-VI-1995, 2♂ 1♀; Spearfish Creek, Hwy 14A, Botany Bay Picnic Area, 13-VII-1997, 1♀; tributary of Bear Butte Creek, Strawberry Picnic Area, 12-VII-1997, 2♂ 2♀. *Pennington Co.:* Beaver Creek, rd 111, Beaver Creek Cmpgd, 16-VII-1997, 1♀; Pine Creek, rd 244, above Horsethief Lake, 5-VI-1995, 1♀, 10-VII-1997, 2♀.

DISCUSSION.—This species is found in the Cascade, Coast, Rocky, and Sierra Nevada Mountains (Baumann et al. 1977). *Sweltsa borealis* seems to prefer small streams in the Black Hills. The Black Hills represent the eastern range limit for this species.

Sweltsa coloradensis (Banks)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Grace Coolidge Creek, 5-VI-1995, 5♂, 10-VII-1997, 92♀; Iron Creek, 6-VII-1968, 2♀ (INHS), 5-VI-1995, 25♂ 6♀, 10-VII-1997, 13♂ 75♀; Little Squaw Creek, 10-VII-1997, 15♀; Spokane Creek, 10-VII-1997, 3♀; Willow Creek, 9-VII-1997, 8♀. *Lawrence Co.:* Black Hills National Forest near Savoy [probably Spearfish Creek], 6-VII-1968, 2♂ 7♀ (INHS); Boxelder Creek, 12-VII-1997, 5♀; East Spearfish Creek, 20-V-1981, 1♀, 7-VI-1995, 30♂ 27♀, 13-VII-1997, 1♂ 64♀; Englewood [probably Whitewood Creek], 18-VI-1925, 2♂ (INHS); Iron Creek, 7-VI-1995, 3♂ 6♀, 13-VII-1997, 8♀; Little Spearfish Creek, 21-V-1981, 2♂, 7-VI-1995, 6♂ 1♀, 13-VII-1997, 7♀; South Fork Boxelder Creek, 12-VII-1997, 17♀; South Fork Rapid Creek, 12-VII-1997, 3♀; Spearfish Creek, 21-V-1981, 3♂, 5-VI-1985, 5♂ 3♀ (INHS), 7-VI-1995, 15♂ 21♀, 13-VII-1997, 1♂ 22♀; Whitetail Creek, 20-V-1981, 22♂ 4♀; Whitewood Creek, 19-V-1981, 3♂ 1♀. *Pennington Co.:* Beaver Creek, 16-VII-1997, 3♀; Deer Creek, 11-VII-1997, 3♀; Grizzly Bear Creek, 5-VI-1995, 4♂ 1♀, 10-VII-1997, 15♀; Palmer Creek, 10-VII-1997, 1♀; Pine Creek, 5-VI-1995, 4♂ 1♀, 10-VII-1997, 16♀; Rapid Creek, 6-VI-1995, 31♂ 7♀, 11-VII-1997, 1♂ 12♀; creek in Sunday Gulch, 9-VII-1997, 46♀; stream in Jenny Gulch, 11-VII-1997, 1♀; Willow Creek, 10-VII-1997, 5♀.

DISCUSSION.—This is another common western North American species, distributed throughout the Coast, Cascade, Sierra Nevada, and Rocky Mountains (Baumann et al. 1977). It is quite common in the Black Hills, with this population representing the easternmost range limit for this species.

Genus *Triznaka*
Triznaka pintada (Ricker)

SOUTH DAKOTA DISTRIBUTION.—*Custer Co.:* Beaver Creek, 4-VI-1995, 9♂ 10♀; Flynn Creek, 9-VII-1997, 2♀; Grace Coolidge Creek, 10-VII-1997, 10♂ 22♀; Iron Creek, 6-VII-1968, 28♂ 51♀ (INHS), 10-VII-1997, 19♂ 71♀; Little Squaw Creek, 15-IX-1970, 1♂* 2♀*, 10-VII-1997, 3♂ 18♀; Spokane Creek, 10-VII-1997, 16♂ 42♀; Sylvan Lake, 20-VI-1940, 2♂ 1♀ (INHS); stream entering Sylvan Lake, 9-VII-1997, 31♂ 21♀; tributary of Beaver Creek, 9-VII-1997, 8♀; Willow Creek, 9-VII-1997, 8♂ 28♀. *Lawrence Co.:* Boxelder Creek, 12-VII-1997, 4♂ 9♀; Englewood [probably Whitewood Creek], 18-VI-1925, 2♂ (INHS, SDSU); Iron Creek, 13-VII-1997, 3♂ 10♀; Jim Creek, 11-VII-1997, 33♂ 30♀; Little Elk Creek, 12-VII-1997, 1♂ 3♀; Little Spearfish Creek, 13-VII-1997, 1♂ 2♀; South Fork Boxelder Creek, 12-VII-1997, 2♂ 8♀; Spearfish Creek, 13-VII-1997, 1♀; tributary of Bear Butte Creek, 12-VII-1997, 6♂ 37♀; tributary of Whitewood Creek, 12-VII-1997, 1♀. *Pennington Co.:* Burnt Fork, 11-VII-1997, 13♂ 26♀; Grizzly Bear Creek, 10-VII-1997, 12♀; Middle Fork Boxelder Creek, 6-VI-1995, 1♀; Newton Fork, 11-VII-1997, 21♂ 45♀; Palmer Creek, 10-VII-1997, 33♂ 31♀; Pine Creek, 10-VII-1997, 1♂ 1♀; Spring Creek, 11-VII-1997, 2♀; creek in Sunday Gulch, 9-VII-1997, 15♂ 17♀; stream in Jenny Gulch, 11-VII-1997, 1♂ 1♀; Willow Creek, 10-VII-1997, 10♂ 8♀.

WYOMING DISTRIBUTION.—*Crook Co.:* Blacktail Creek, 16-VII-1997, 1♂ 10♀; T52N R63W [probably Houston Creek], 22-VII-1982, 1♂ 3♀; Whitelaw Creek, 16-VII-1997, 18♂ 43♀. *Weston Co.:* Cold Creek, 16-VII-1997, 6♂ 7♀.

DISCUSSION.—This species, often confused with *T. signata*, occurs in the Coast, Cascade, Sierra Nevada, and Rocky Mountains, but it has not been reported from Canada (Baumann et al. 1977, Stark et al. 1986). *Triznaka pintada* is very common in the Black Hills, with this area representing the easternmost range limit for this species.

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RIPARIAN VEGETATION ALONG THE MIDDLE SNAKE RIVER, IDAHO: ZONATION, GEOGRAPHICAL TRENDS, AND HISTORICAL CHANGES

Mark D. Dixon[1,2] and W. Carter Johnson[1]

ABSTRACT.—A baseline study was conducted on an 83-km free-flowing reach of the Snake River between Swan Falls Dam and the Idaho-Oregon border. The research had 2 components: (1) field characterization and inventory of existing riparian flora, vegetation, and environment (soils, topography, streamflow), and (2) determination and mapping, using a geographic information system, of historic changes in riparian vegetation based on a time series (1938–39, 1957, 1969, 1987) of aerial photographs.

The flora was diverse, with 185 species of vascular plants identified, 63 of which were exotics. Vegetation was structured vertically along the riverbank gradient into lifeform-defined habitat types: emergent, riparian shrub-forb, tree, transitional grass-shrub, and upland. Riverbank seepage, probably of agricultural origin, blurred zonation patterns on some sites and added species to the overall flora. Upstream-downstream differences existed in the physical characteristics and vegetation of river subreaches.

Coverage of riparian woodland, island riparian and total riparian vegetation, and area of islands increased since the 1930s, with the greatest changes in the 1969–1987 interval. Possible contributing factors were (1) significant declines in annual minimum flows since the 1950s, (2) decreases in peak flows following completion of Swan Falls Dam and some upstream dams since the 1920s, (3) introduction and spread of exotic tree species (*Elaeagnus angustifolia* and *Tamarix* spp.), and (4) possible effects of intensive agriculture on river sediment load and soil nutrients. The introduction and proliferation of purple loosestrife (*Lythrum salicaria*) could have considerable future effects on vegetation-channel dynamics in the middle Snake River.

Key words: exotic species, GIS, Lythrum salicaria, *vegetation dynamics, landscape change.*

Rivers are the lifeblood of the semiarid western United States, providing water for irrigation, livestock, hydroelectric power, and recreation (Thomas et al. 1979, Graf 1985). Rivers and their associated riparian zones also provide valuable habitat for fish and wildlife species, enhancing biodiversity at local and regional scales (Odum 1979, Knopf et al. 1988, Naiman et al. 1993). This diversity of uses stretches the ability of western rivers to sustain all demands, creating conflicts among different resource users. As a result, riparian ecosystems throughout much of the West have been modified through alterations in riverine flow regime and geomorphic processes through dam operation (Nadler and Schumm 1981, Rood and Mahoney 1990, Johnson 1991, 1992); immersion by reservoir construction (Ohmart et al. 1988); damage from excessive livestock use (Kauffman and Krueger 1984) or human recreation (Ohmart et al. 1988); clearing for agriculture (Hoar and Erwin 1985), industry, residential areas, and road-building (Ohmart et al. 1988); and invasion by exotic plant species (Christensen 1962, 1963, Horton 1977, Graf 1978, Blackburn et al. 1982, Knopf and Olson 1984, Brotherson and Field 1987, Howe and Knopf 1991, Brock 1994).

The Snake River, like most other large western rivers, has undergone major modifications and is at the center of water-use controversy (Palmer 1991, Anglin et al. 1992, Kjelstrom 1992). Since the mid-1800s parts of the Snake River plain have been transformed from sagebrush cold desert to thriving agriculture through irrigation. A series of mainstem dams on the river impound water for irrigation storage and hydroelectric power generation. The Snake River also has important biotic resources. The Snake River Birds of Prey Conservation Area (SRBPCA) contains the highest concentration of noncolonial nesting raptors of any location in the world (Kochert and Pellant 1986). Lower reaches of the river are an essential migratory route for the endangered Snake River chinook salmon, and important fisheries exist along several sections of the river for white sturgeon, a species of concern (Anglin et al. 1992). Islands in the river provide nesting areas for geese and ducks, as well as for colonial wading birds and gulls. Finally, the river provides a green band of riparian shrub and woodland habitat in an otherwise arid landscape.

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Despite the economic and biotic resources of the Snake River, surprisingly little research has been conducted on its ecology. This paper provides baseline ecological information on the riparian zone of the middle Snake River from Swan Falls Dam downstream to the Idaho-Oregon border. The research had 2 components: (1) field characterization and inventory of the existing riparian vegetation and environment, and (2) determination and mapping of historic changes in riparian vegetation based on a time series of aerial photographs, using a geographic information system (GIS). This information was needed to make an initial assessment of the effects of possible flow reductions on the composition and distribution of riparian vegetation and on the integrity of islands used by nesting waterfowl (Johnson et al. 1995).

STUDY AREA

The study area is an 83-km section of the Snake River from Swan Falls Dam to the Idaho-Oregon border (Fig. 1). This section is part of the longest free-flowing stretch of the river, beginning at Swan Falls Dam and continuing to Brownlee Reservoir approximately 185 km downstream. Most of the islands in this section lie within the Deer Flat National Wildlife Refuge and the SRBPCA. Except for the SRBPCA, most of the mainland banks are privately owned.

Swan Falls Dam, begun in 1901 and completed by 1918, is the oldest dam on the Snake River. Several much larger reservoirs occur upstream of the study area, including American Falls (completed in 1927) and Palisades (completed in 1957). Both reservoirs have storage capacities of >1.4 million acre-feet (1.7 billion m^3; Brennan et al. 1996).

The study area lies within the Columbia–Snake River Plateau Physiographic Province of the northern Great Basin or Intermountain region, characterized by hot, dry summers and cold winters (West 1981). Native upland vegetation is intermountain sagebrush steppe and intermountain salt-desert shrubland (Küchler 1964, West 1981) dominated by big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), greasewood (*Sarcobatus vermiculatus*), fourwing saltbush (*Atriplex canescens*), Great Basin wild rye (*Elymus cinereus*; botanical nomenclature follows Hitchcock et al. 1955–1969 or Great Plains Flora Association 1986). Many exotic species, in particular cheatgrass (*Bromus tectorum*), have become dominant in this region. Woody riparian vegetation in the study area is dominated by coyote willow (*Salix exigua* subsp. *exigua*), peachleaf willow (*Salix amygdaloides*), Russian olive (*Elaeagnus angustifolia*), and tamarisk or saltcedar (*Tamarix* spp.).

Topography and surficial geology change longitudinally through the study area (Kjelstrom 1992). For the first several kilometers downstream from Swan Falls, the river is constrained by steep canyon walls topped with basalt, rising up to 200 m above the river. The canyon widens out near Guffey Bridge (north of Murphy, Fig. 1), where the first islands in Deer Flat National Wildlife Refuge begin. Downstream from Guffey Bridge the river widens and decreases in gradient. Parts of the river and surrounding plain are bordered by canyon walls (generally the north side) up to the town of Marsing. From Marsing to the Idaho-Oregon border the river is not canyon-walled but is bounded by relict terraces shaped by the catastrophic Bonneville Flood event, 15,000 B.P. (Othberg 1994).

Because of these longitudinal gradients (upstream-downstream), the study area was divided into 4 reaches, each containing 10 sample cross sections for vegetation sampling and hydrologic analysis. The first reach (canyon-walled area) covers the 18 km downstream from Swan Falls Dam, ending just beyond Guffey Bridge (Fig. 1). Reach 2 covers the next 22 km to a location between Walters Ferry and Marsing. Reach 3 covers the next 20 km to Marsing, and reach 4 covers the 23 km from Marsing to the Idaho-Oregon border.

Human impacts on the riparian zone and bordering uplands vary across the study area, with land cover by intensive agriculture and residential development increasing progressively downstream. Livestock grazing has probably been a pervasive feature throughout the area for almost 300 yr, intensifying with settlement by white immigrants around the 1860s

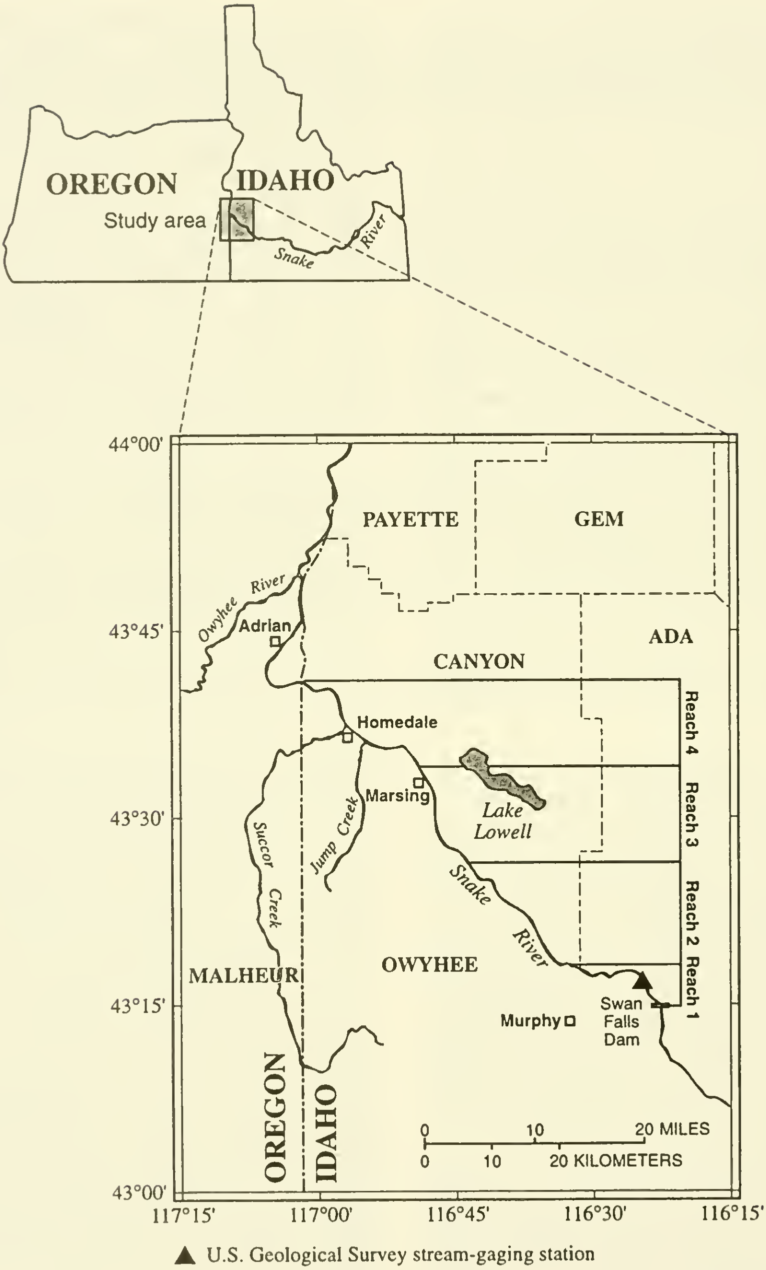
OREGON
IDAHO
Study area
Snake River
44°00'
43°45'
43°30'
43°15'
43°00'
117°15'
117°00'
116°45'
116°30'
116°15'
PAYETTE
GEM
ADA
CANYON
Owyhee River
Adrian
Homedale
Marsing
Lake Lowell
Jump Creek
Succor Creek
Snake River
OWYHEE
MALHEUR
Murphy
Swan Falls Dam
Reach 4
Reach 3
Reach 2
Reach 1
OREGON
IDAHO
0 10 20 MILES
0 10 20 KILOMETERS
▲ U.S. Geological Survey stream-gaging station

Fig. 1. Map of the study area delineating study reaches (adapted from Kjelstrom 1992).

(Yensen 1980). Current land use is dominated by irrigated agriculture, pasture and open range grazing, and residential development. Recreational uses of the river include fishing, hunting, and boating, especially in the downstream reaches.

METHODS

Vegetation Sampling

We sampled riparian vegetation along 40 river cross sections 20 June–17 September 1990. Sites were chosen randomly within each

2-km segment of the river from cross sections previously surveyed and monumented by the United States Geological Survey (USGS; Kjelstrom 1992). USGS cross sections occurred at approximately 0.3-km intervals throughout the study reach. Sites severely disturbed by human activities were not selected. Transects began in shallow water and extended up the bank until reaching upland vegetation (shrub-steppe or human-developed).

To avoid areas where vegetation had been disturbed by the USGS survey, we offset the vegetation transect approximately 10 m from the USGS cross section. We sampled the herb layer (<1 m tall) in continuous (1 m × 1 m) quadrats (except across some flat island surfaces on which quadrats were sampled at intervals). The 2 dominant (on the basis of cover) herbaceous species and all species of tree seedlings were recorded in each quadrat. Percent cover of tamarisk seedlings and purple loosestrife (*Lythrum salicaria*) was estimated to the nearest 10% (with a 1% category for trace coverage) separately within each quadrat.

We classified each quadrat in the field as 1 of 5 vegetation types (Johnson et al. 1995) based on the bank/gradient position of the quadrat and composition and physiognomy of vegetation. Types were emergent/ephemeral, riparian shrub-forb, tree, transitional grass-shrub, and upland vegetation. For each site we noted signs of past disturbance and the presence of surface moisture from bank seepage.

Shrub layer cover was measured along the main transect and on 2 parallel transects offset 3 m to each side. Shrubs were defined as woody vegetation >1 m in height and with a basal trunk diameter <10 cm. The presence of shrub cover vertically intersecting each transect was recorded by species along each m.

We quantified density and basal area of trees (≥10 cm diameter) within a belt transect centered on the main transect. When large numbers of trees were present, we used a narrower (10- or 20-m-wide) belt; when trees were sparse, a 40-m-wide belt. Trunk diameter was measured at or near the base of the tree but above any basal swelling. Individual trunks that were separated at ground level were treated as separate trees.

We surveyed the elevation of the water surface, the center of each quadrat, and reference posts of known elevation from the USGS cross sections (to the nearest 0.003 m). This enabled us to relate positions on the vegetation transect to the USGS cross section and to water surface elevation estimates for different flows. All elevations were later scaled relative to water surface elevation (WSE) at a discharge of 339 cms (11,974 cfs), the annual mean discharge for the previous 25 yr (1966–1990 inclusive) at the USGS gage near Murphy, Idaho (EarthInfo 1991). This provided a common reference flow and a basis for comparison of elevations across sites and sampling dates. Water surface elevation at mean discharge was estimated by modeling the relationship of river stage to different discharge levels for each cross section (Kjelstrom 1992, Auble et al. 1994, Johnson et al. 1995). Flows during the summer of 1990 when fieldwork was conducted averaged 196 cms (mean of mean monthly flows for June–September 1990), substantially lower than the 25-yr mean annual discharge.

Soil Sampling and Analysis

Using an 8.3-cm bucket auger, we took soil cores at depths of 0–20 cm and 20–40 cm at 2-m intervals along each vegetation transect. Soil samples were analyzed for pH; percent organic matter; nitrate-nitrogen, phosphorus, and potassium concentrations (ppm); and salinity (mmho/cm). Texture was assessed by hand as fine, medium, or coarse. For statistical analyses, we used only 3 cores (upper, middle, and lower slope positions) per bank, with data from the 2 depths combined (averaged).

Organic matter (readily oxidizable) was determined using a loss-on-ignition procedure and nitrate-nitrogen by a colorimetric method utilizing salicylic acid (USDA 1996), since high salt levels interfered with electrode readings for nitrogen. Available phosphorus was estimated colorimetrically using the Bray and Kurtz no. 1 extraction with a 1:10 (w/v) soil-to-solution ratio, and available potassium by extraction with ammonium acetate and a flame emission test. Measurements of pH were made with a glass electrode using a 1:1 (w/v) soil-to-water ratio on a stirred sample. Soluble salts were estimated using a conductivity cell and a 1:1 soil-to-water extract.

Riverbed Sediment Sampling

We collected a total of 154 samples of riverbed substrate near 45 cross sections. Samples were collected within several meters of the riverbank using a hand spade. Data from multiple samples or samples at different depths (surface or subsurface) at individual banks were averaged to yield 86 samples for statistical analysis.

The particle size distribution of each sample was determined by passing the sample through sieves. Sieve sizes (in mm) and particle size classes were delineated as follows: <0.0625, silt; 0.0625–2.0, sand; 2.0–64.0, gravel; 64.0–256.0, cobble; and >256.0, boulders. The D50, or particle diameter at which 50% of the sample (by mass) would be retained and 50% passed, was estimated by visually interpolating from the particle size distribution curves.

Current and Past Vegetation Coverage

Aerial photographs from the years 1938–39 (b/w), 1957 (b/w), 1969 (b/w), and 1987 (false color) were obtained for the study area. All photographs were printed at a scale of 1:7920 from an original scale of 1:20,000 and 1:40,000 for the 1938–1969 and 1987 photographs, respectively. Most photographs were taken during the growing season (leaf on). Flows at the Murphy gage ranged from 159 to 232 cms for the 1987 series, 408 cms for 1969, 204 to 225 cms for 1957, and 203 to 305 cms for 1938–39.

Land and water cover extending to 0.4 km beyond the outer banks was digitized from the 1987 color infrared photographs. For older black-and-white photographs, we delineated and digitized only riverine and riparian cover types. The narrowness of riparian vegetation usually precluded distinguishing elevational zones. Cover types were assigned based on the dominant vegetation along a bank segment.

Photograph coverages were digitized using the PC ARC/INFO (ESRI 1991) Geographic Information System (GIS). Areal coverage of the different habitat types was tallied within the 4 reaches of the river and compared among the 4 photographic dates. Accuracy of habitat classifications was checked in the field (Johnson et al. 1995).

RESULTS

Physical Characteristics

Physical characteristics of the river channel and banks change significantly from reach 1 to the reaches further downstream. River cross sections in reach 1 averaged significantly ($P \leq 0.05$) narrower and deeper, with steeper gradient, than reaches further downstream (Table 1). Also, the proportion of mainland banks with seepage increased downstream. Seeps formed a heterogeneous category varying from hillsides moist from subsurface seepage to areas with flowing irrigation return water. Seeps were not found on any reach 1 sites, yet were present on 38% of the mainland banks in the lower 3 reaches (Table 1). Size of the bed material generally decreased downstream also, with significantly higher silt content and lower D50 (median particle size by weight) in reach 4 sites than reach 1. Median particle size was in the gravel size range (2.0–64.0 mm diameter) for all reaches except reach 4.

Quantities of most soil nutrients, salts, and organic matter were higher in reaches 2–4 than reach 1 and appeared to be highest in reach 4 (Table 2). Concentrations were generally higher on mainland banks than on island banks; within mainland banks, concentrations were higher on sites identified as seeps than on nonseeps (Table 3).

Hydrologic Record

Mean daily flows averaged 316 cms on an annual basis over 77 yr of record (1914–1990) for the Murphy gage (Fig. 2). The mean annual peak flow was 667 cms, and the mean annual minimum flow was 182 cms. Annual minimum and maximum flows varied approximately over a 4-fold range on average, and a 10-fold range for the minimum (128 cms) and maximum (1305 cms) daily flows of the 77-yr record. Minimum flow shows a significant, yet weak, negative correlation with year of record ($R = -0.35$, $P = 0.0019$). However, the flow record suggests an increase in minimum flows until the 1950s, with decreases thereafter (Fig. 2). Minimum flows were positively associated with year of record from 1914 to 1957 ($R = 0.72$, $P = 0.0001$), but negatively associated from 1958 to 1990 ($R = -0.70$, $P = 0.0001$). This shift in minimum flows coincides with the completion of Palisades Reservoir, far upstream in eastern Idaho, in 1957 (Brennan et al. 1996). Minimum flows were particularly low from the early 1970s to present day, with 16 of the 20 lowest annual minimum flows on record occurring between 1973 and 1990.

Peak flows may have declined from the predam to early post-dam period. The 4 highest annual peak flows all occurred in the first 8 yr

TABLE 1. Physical characteristics of the 4 study reaches, based on 10 sampled cross sections in each. Within a column, different letters designate significant differences from ANOVA and least squares means (SAS Institute 1985) pairwise comparisons ($P \leq 0.05$).

Reach	Stream gradient (m/km)*	% seep main banks	Riverbed sediments** N	% silt	% sand	% gravel	D50 (mm)	Mean max.*** depth ± $s_{\bar{x}}$ (m)	Mean channel*** width ± $s_{\bar{x}}$ (m)
1	0.63	0	10	1.8 ± 0.6 (0.6)^{a}	42.8 ± 12.6 (16.3)	51.9 ± 12.7 (67.0)	20.5 ± 8.1 (16.3)^{a}	6.55 ± 1.19^{a}	136.9 ± 17.0^{a}
2	0.36	30	18	5.0 ± 1.5 (1.0)^{ab}	46.8 ± 8.7 (24.9)	46.6 ± 9.5 (59.2)	10.1 ± 2.3 (10.2)^{ab}	3.30 ± 0.43^{b}	212.7 ± 18.1^{b}
3	0.20	50	13	4.0 ± 1.8 (1.6)^{a}	29.7 ± 7.6 (17.7)	65.7 ± 8.7 (72.9)	17.0 ± 3.7 (13.4)^{a}	3.35 ± 0.36^{b}	264.4 ± 32.1^{b}
4	0.26	35	45	10.2 ± 1.8 (6.4)^{b}	52.0 ± 4.7 (57.1)	37.8 ± 5.7 (27.5)	7.1 ± 1.4 (0.5)^{b}	3.35 ± 0.34^{b}	242.1 ± 22.0^{b}
ALL	0.33	29	86	7.2 ± 1.1 (2.5)	46.4 ± 3.6 (35.0)	45.5 ± 4.1 (58.3)	10.8 ± 1.5 (5.8)	4.14 ± 0.39	214.1 ± 13.5

*Distances and elevations estimated from Kjelstrom (1992).

**Means ± $s_{\bar{x}}$ and medians (in parentheses) of sediment characteristics. Medians compared via ANOVA on ranked data. The model included REACH, SITE(REACH), and LANDFORM (island or mainland). Reach differences were tested via least squares means procedure on ranks using SITE(REACH) as the error term.

***Mean maximum depth and mean channel width compared among reaches via 1-way ANOVA and least squares means procedure (SAS Institute 1985)

TABLE 2. Means ± $s_{\bar{x}}$ and medians (in parentheses) of soil characteristics by reach. Organic matter (% OM) expressed as percent of sample by weight; nitrate-nitrogen (NO_3–N), phosphorus (P), and potassium (K) expressed as ppm; SALTS (conductivity) expressed as mmho/cm. Comparisons of medians were made via ANOVA* and least squares means (SAS Institute 1985) on ranked data. Within rows, different letters represent significant differences ($P \leq 0.05$) in pairwise comparisons.

	Reach				
Soil characteristic	1 (N = 73)	2 (N = 84)	3 (N = 75)	4 (N = 76)	2–4 combined (N = 235)
% OM	1.40 ± 0.20 (1.00)^{a}	1.56 ± 0.12 (1.28)^{ab}	1.66 ± 0.16 (1.25)^{ab}	1.89 ± 0.15 (1.60)^{b}	1.70 ± 0.08 (1.40)**
NO_3–N***	13.84 ± 2.56 (6.20)^{a}	15.93 ± 2.93 (8.05)^{ab}	23.97 ± 6.56 (10.20)^{b}	21.89 ± 4.38 (8.20)^{b}	20.42 ± 2.73 (8.60)**
P	15.51 ± 1.89 (10.50)	16.41 ± 1.96 (11.50)	19.87 ± 2.49 (11.50)	26.10 ± 6.95 (10.00)	20.65 ± 2.49 (11.00)
K	498.4 ± 71.0 (290.0)^{a}	737.2 ± 96.4 (365.0)^{b}	756.8 ± 157.0 (450)^{bc}	712.8 ± 69.1 (526.3)^{c}	735.6 ± 64.5 (435.0)**
pH	8.17 ± 0.04 (8.10)	8.22 ± 0.06 (8.10)	8.20 ± 0.05 (8.10)	8.29 ± 0.07 (8.20)	8.24 ± 0.03 (8.10)
SALTS	1.55 ± 0.28 (1.10)^{a}	2.92 ± 0.42 (1.7)^{b}	2.98 ± 0.51 (1.30)^{b}	3.01 ± 0.40 (1.90)^{b}	2.97 ± 0.26 (1.5)**

*Two-way fixed-effects ANOVA model included REACH and SLOPE (slope position: lower, middle, upper) as factors.

**Difference between reach 1 and combination of reaches 2–4 is statistically significant ($P \leq 0.05$).

***P = 0.054 for NO_3–N ANOVA model.

TABLE 3. Means ± $s_{\bar{x}}$ and medians (in parentheses) of soil characteristics on nonseep main banks, seep main banks, and island banks. Organic matter (% OM) expressed as percent of sample by weight; nitrate-nitrogen (NO_3–N), phosphorus (P), and potassium (K) expressed as ppm; SALTS (conductivity) expressed as mmho/cm. Comparisons of medians were made via ANOVA* and least squares means (SAS Institute 1985) on ranked data. Within rows, different letters represent significant differences ($P \leq 0.05$) in pairwise comparisons.

	Landform		
Soil characteristic	Nonseep main (N = 164)	Seep (N = 67)	Island (N = 77)
% OM	1.59 ± 0.11 (1.30)^{a}	2.24 ± 0.21 (1.80)^{b}	1.17 ± 0.09 (1.00)^{c}
NO_3–N	14.89 ± 1.8 (6.80)^{a}	39.54 ± 8.32 (18.40)^{b}	9.33 ± 1.20 (6.20)^{a}
P	20.56 ± 3.25 (11.00)	24.42 ± 3.79 (12.00)	12.70 ± 1.24 (9.50)
K	643.9 ± 47.6 (442.5)^{a}	1152 ± 196.4 (600.0)^{b}	343.8 ± 24.8 (255.0)^{c}
pH	8.26 ± 0.04 (8.20)^{a}	8.27 ± 0.09 (8.10)^{a}	8.11 ± 0.03 (8.10)^{b}
SALTS	2.92 ± 0.32 (1.40)^{a}	3.29 ± 0.50 (1.80)^{b}	1.45 ± 0.13 (1.10)^{c}

*Two-way fixed-effects ANOVA model included LANDFORM and SLOPE (slope position: lower, middle, upper) as factors.

of record (1914, 1917, 1918, 1921), prior to the filling of American Falls Reservoir in 1927 (Brennan et al. 1996). Peak flows in the interval, 1914–1926, averaged higher than peak flows in 1928–1956 and 1958–1990 (Table 4), but the difference was only marginally significant for 1914–1926 vs. 1958–1990 (P = 0.0519). In contrast, minimum flows were significantly higher in 1928–1956 than in either 1914–1926 or 1958–1990.

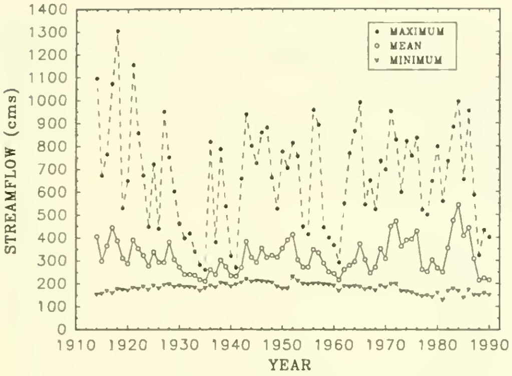

Fig. 2. Hydrologic record showing annual maximum, mean, and minimum daily flows (cms) of the Snake River at the USGS gage near Murphy, Idaho. Years represent water years (October to September).

Vegetation Composition and Zonation

The flora of the riparian zone was relatively rich, with 185 species collected or observed, 63 of which were exotics. Most exotics (55) were of Eurasian origin and have been naturalized, while a few (8) were adventive species native to elsewhere in North America. Exotics included several very common species: *Polypogon monospeliensis, Bromus tectorum, Lythrum salicaria, Solanum dulcamara, Tamarix* spp. (*T. chinensis* and *T. ramosissima*; these were not distinguished in the field), and *Elaeagnus angustifolia*. Approximately 2/3 of tree density and basal area was made up of exotics, with *Celtis reticulata* and *Salix amygdaloides* the only regionally native tree species encountered during sampling. The most ubiquitous plant species included *Salix exigua* among shrubs; *Euthamia occidentalis* among forbs; *Polypogon monospeliensis, Bromus tectorum,* and *Distichlis spicata* var. *stricta* among grasses; *Eleocharis erythropoda* among emergents; and *Elaeagnus angustifolia, Tamarix* spp., and *Salix amygdaloides* among trees (Table 5).

On nonseep sites riparian vegetation occurred in structurally distinct vertical zones above mean river level (Fig. 3; Johnson et al. 1995). Elevation ranges that follow are averages across all nonseep sites, not deterministic patterns that will hold on all sites. These were defined, from lowest to highest, as emergent/ephemeral (approx. –0.6 to –0.3 m) dominated by wetland emergent plants (*Scirpus, Eleocharis, Polygonum*), wetland grasses (*Polypogon, Paspalum, Leptochloa*), and some annuals (*Bidens, Chenopodium*) that colonize disturbed shoreline/sandbar conditions; riparian shrub-forb (–0.3 to 0.8 m) dominated primarily by perennial herbaceous plants (*Euthamia occidentalis, Solanum dulcamara, Phalaris arundinacea*) and willow (*Salix exigua*) thickets; tree (0.8 to 1.4 m) dominated by *Salix amygdaloides, Tamarix,* and *Elaeagnus*; transitional grass-shrub (1.4 to 1.8 m) comprising various species, including several grass species (*Distichlis spicata, Bromus tectorum, Elymus triticoides*), weedy forbs (*Kochia scoparia, Salsola iberica, Cardaria draba*), and/or shrubs (*Rosa woodsii, Toxicodendron rydbergii, Rhus aromatica*); and upland (>1.8 m) dominated by *Artemisia tridentata, Sarcobatus vermiculatus, Chrysothamnus* spp., and *Atriplex canescens.* Much upland was farmed in downstream areas, with the native vegetation severely disturbed

TABLE 4. Comparison of annual means ± $s_{\bar{x}}$ of maximum, minimum, and mean daily flows (cms) for 3 intervals of water years: 1914–1926 (before American Falls Reservoir), 1928–1956 (after American Falls, before Palisades Reservoir), and 1958–1990 (after Palisades Reservoir). The years during which the dams at American Falls and Palisades were completed (1927 and 1957, respectively) are excluded from the analysis. Different letters within a row represent significant differences ($P \leq 0.05$) of flow among year intervals from 1-way ANOVA and least squares means (SAS Institute 1985) pairwise comparisons.

	Water year intervals		
	1914–1926	1927–1956	1958–1990
Mean flow*	343.9 ± 19.5^{a}	294.4 ± 13.3^{b}	323.6 ± 12.4^{b}
Maximum flow**	799.0 ± 61.9^{a}	604.8 ± 41.4^{b}	654.6 ± 38.8^{b}
Minimum flow	174.5 ± 4.5^{a}	197.2 ± 3.0^{b}	170.8 ± 2.8^{a}

*ANOVA model for mean flow significant at $P = 0.0892$.
**Pairwise comparison between 1914–1926 and 1958–1990 intervals significant at $P = 0.052$.

TABLE 5. Most ubiquitous vascular plant species by lifeform group. Top 8 species (per group) with at least 10% occurrence (detected at 4 of the 40 sampling sites or cross sections) are listed[a].

Lifeform group/ Species	% of cross sections
EMERGENTS	
Eleocharis erythropoda	78
Scirpus acutus	45
Scirpus pungens	45
Juncus torreyi	35
Typha latifolia	35
Scirpus validus	10
GRASSES	
Polypogon monospeliensis	80
Bromus tectorum	78
Distichlis spicata	73
Paspalum distichum	60
Phalaris arundinacea	58
Elymus triticoides	48
Hordeum jubatum	30
Agropyron intermedium	25
Carex lanuginosa	25
FORBS	
Euthamia occidentalis	90
Solidago gigantea	60
Solanum dulcamara	60
Lythrum salicaria	53
Kochia scoparia	48
Apocynum cannabinum	45
Urtica dioica	45
Cardaria draba	40
SHRUBS	
Salix exigua	83
Ribes aureum	58
Sarcobatus vermiculatus	50
Rosa woodsii	40
Toxicodendron rydbergii	23
Rhus aromatica	20
Artemisia tridentata	20
Atriplex canescens	20
Suaeda torreyana	20
TREES	
Elaeagnus angustifolia	60
Tamarix spp.	58
Salix amygdaloides	53
Ulmus pumila	30
Populus deltoides	20
Fraxinus pennsylvanica	15
Celtis reticulata	10

[a] Not all groups had 8 species with at least 10% occurrence. Also, 2 groups list 9 species because of ties in % occurrence.

or absent. Most islands also did not contain true upland shrub habitats but had dry grassland and forb interiors similar to the transitional grass-shrub habitat.

Longitudinal patterns for trees and purple loosestrife paralleled those of gradient, seepage, and sediment size. Loosestrife, absent from sites sampled in reach 1, was abundant downstream, particularly in reach 4 (Fig. 4). Tree diversity, density, and occurrence were low in reach 1, generally increasing downstream (Figs. 4, 5). Groves of *Celtis reticulata* occurred only on reach 1 sites. Other tree species (*Elaeagnus*, *Salix amygdaloides*, and *Tamarix*) did not become common until reach 2.

Seeps

Seepage greatly altered vertical zonation patterns of vegetation, sometimes allowing lush herbaceous growth and occurrence of wetland obligate plants far upslope. Thickets of shrubs sometimes occurred high on mainland banks above seeps, and a few seep sites had trees (in particular *Elaeagnus*) growing much higher than on nonseep banks. Most seep sites, however, had little woody vegetation.

Seeps added diversity to the overall flora, since several species were confined to seeps and others were most abundant on seeps. Purple loosestrife and *Solanum dulcamara* were the 2 most common dominants on seep sites, followed by *Urtica dioica*, *Phalaris arundinacea*, and *Euthamia occidentalis*. Analysis of frequency of occurrence showed that loosestrife occurred on a significantly higher proportion ($P \leq 0.05$) of seep banks (12 of 23) than nonseep banks (22 of 85; Table 6), and seep quadrats (80 of 407) than nonseep quadrats (74 of 1502; $\chi^2 = 93.677$, $P < 0.001$). *Phalaris*, *Solanum*, and *Nasturtium officinale* also occurred as quadrat dominants on a significantly higher proportion of seep banks than nonseep banks ($P \leq 0.05$). *Mimulus guttatus* and *Nasturtium* occurred almost exclusively on seeps. Other species more common on seeps than on nonseeps included *Veronica anagallis-aquatica*, *Typha latifolia*, *Lycopus asper*, *Scirpus americanus*, and *Phragmites australis*.

Areal Coverage of Habitats

CURRENT VEGETATION EXTENT.—Riparian vegetation covered approximately 388 ha in 1987 (Table 7), averaging 4.7 ha/km of river. Riparian shrub (223 ha) dominated the riparian zone, followed by dense woodland (68 ha), riparian herbaceous (47 ha), and open woodland (45 ha). About 2/3 of all riparian habitat was on mainland sites (258 ha), with 1/3 on islands (129 ha). Riparian habitats covered approximately 44% of total island area. Upland vegetation occupied 48%, with agriculture (cropland, irrigated pasture, farmsteads) occupying

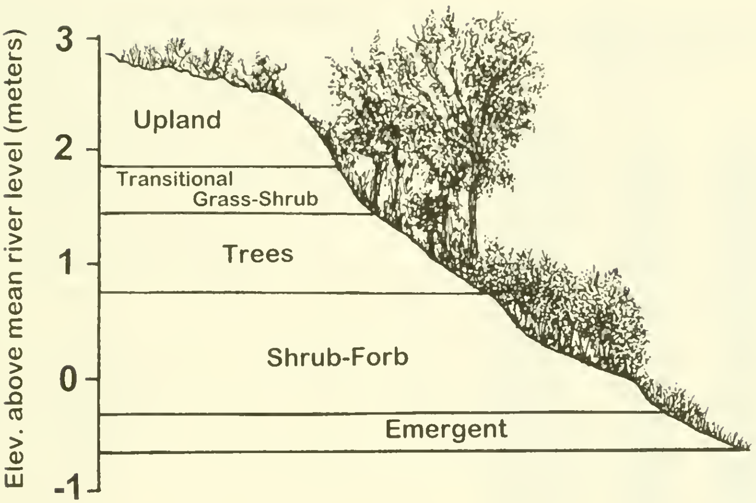

Fig. 3. Schematic of vertical zonation of riparian vegetation types (adapted from Johnson et al. 1995).

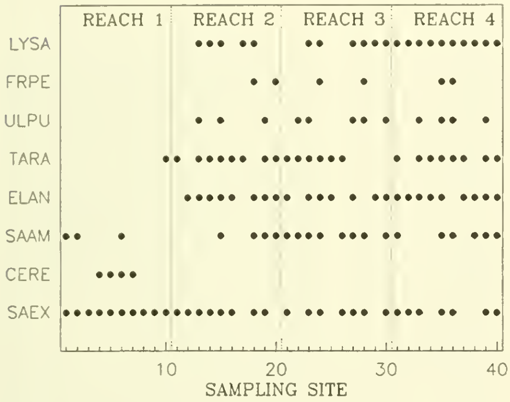

Fig. 4. Geographic distribution of selected species among sampling sites within the study area from Swan Falls Dam to the Idaho-Oregon border. Filled dots represent occurrence of a species on a sampling site. Species mnemonics represent the following: LYSA = *Lythrum salicaria*, FRPE = *Fraxinus pennsylvanica*, ULPU = *Ulmus pumila*, TARA = *Tamarix* spp., ELAN = *Elaeagnus angustifolia*, SAAM = *Salix amygdaloides*, CERE = *Celtis reticulata*, and SAEX = *Salix exigua*.

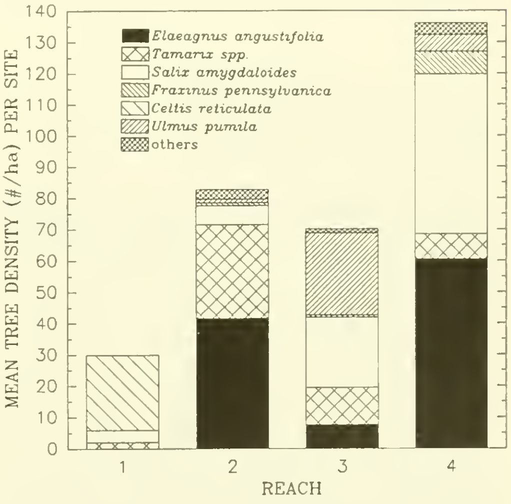

Fig. 5. Mean density of trees (# trees/ha) per site across the 4 study reaches. Densities are based on the total number of trees on each site (cross section) divided by the total area of tree-sampling plots (individual banks pooled) per site.

another 9%. Riparian vegetation of islands was composed of a higher percentage of riparian shrub (65%) and dense woodland (23%), and lower percentage of herbaceous riparian (3%), than was the riparian zone on mainland banks (54%, 15%, and 17%, respectively).

Nonriverine areas were dominated by upland vegetation (3701 ha) and cropland (2931 ha), followed by towns and residential areas combined (132 ha), nonriparian (nonriverine) wetland categories and ponds (134 ha), and minor categories (severely impacted areas, planted trees, farmsteads etc.).

The relative proportion of upland to cropland changed longitudinally (Fig. 6). Upland vegetation covered nearly 95% of the nonriver area of reach 1, with intensive agriculture occupying less than 1%. Coverage by agriculture

TABLE 6. Presence and absence of species as quadrat dominants on all seep and nonseep banks. Results in parentheses indicate continuity-adjusted chi-square analyses.

	Banks					
	Nonseep		Seep		χ^2	
Species	Presence	Absence	Presence	Absence	(1 df)	*P*
*Epilobium ciliatum**	2	83	5	18	11.224 (8.253)	0.001 (0.004)
Lythrum salicaria	22	63	12	11	5.801 (4.646)	0.016 (0.031)
*Nasturtium officinale**	1	84	10	13	35.410 (30.937)	<0.001 (<0.001)
Phalaris arundinacea	19	66	10	13	4.113 (3.844)	0.043 (0.078)
Solanum dulcamara	21	64	14	9	10.807 (9.220)	0.001 (0.002)
*Urtica dioica**	7	78	11	12	20.429 (17.678)	<0.001 (<0.001)

*25% of the cells have expected counts <5. Chi-square should be interpreted with caution.

increased to 65% in reach 4. Proportional coverage by riparian habitat also increased slightly downstream, from about 4% in reach 1 to 6% in reach 4.

Composition of riparian vegetation also changed downstream (Fig. 7, 1987 data). Riparian vegetation in reach 1 was primarily riparian shrub (approx. 70%) and riparian herbaceous (26%). Woodland coverage increased greatly downstream, from almost nonexistent in reach 1 to 53 ha (43% of the riparian zone) in reach 4. This matched the general pattern observed for trees from the transect data.

Classification accuracy for the 1987 photographs was 85.7% among riparian categories, or 74.8% when adjusted for chance agreement; and 89.9%, or 88%, respectively, for all polygons (Table 8). Actual error rates are lower, since classification errors detected during ground-truthing were corrected on the final computer files and maps.

TEMPORAL CHANGE IN VEGETATION.—Area of riparian habitat categories changed both in time and space (Fig. 7). The most striking feature was the temporal increase in woodland area in reaches 2–4, and no change or a slight decrease in reach 1. Woodland increased on both main and island banks, with especially large increases in the dense woodland category (Fig. 8). Woodland area increased nearly 3-fold (3.5-fold if *Celtis* woodlands are excluded) between 1938–39 and 1987. The increase in woodland area (as a percentage of beginning woodland area) appeared to be relatively consistent over the whole time series: an approximate 2.9% increase per year for 1939–1957, 2.6%/yr for 1957–1969, and 2.5%/yr for 1969–1987. Both open woodland and dense woodland increased in area. Open woodland increased only slightly on islands, but dense woodland increased nearly 20-fold, from only 1.5 ha in 1939 to 29.5 ha in 1987. On mainland banks open woodland increased from 14 ha to 33 ha, while dense woodland increased from 6 ha to 39 ha.

Total riparian area also increased over time, from 365 ha in 1938–39 and 1957 to 388 ha in 1987 (Figs. 7, 9). The anomalous decline in total habitat in 1969 is probably due to riparian herbaceous habitat being covered by higher flows in the river on the date of the photograph. Virtually all of the increase in total riparian area was due to expansion of island riparian vegetation between 1969 and 1987 (from 102 to 129 ha), and the largest increases occurred in reach 4 (Fig. 7d). Across the time series, the increase in riparian woodland (76 ha) far exceeded that of total riparian area, suggesting that most woodland expansion occurred through secondary succession within

TABLE 7. Area of land cover classes for 1987 GIS coverage, middle Snake River.

Land/water cover categories	Area (ha)
Riparian herbaceous—mainland banks	44.0
Riparian herbaceous—island banks	3.5
Riparian shrub—mainland banks	138.7
Riparian shrub—island banks	84.1
Riparian open woodlands—mainland banks	33.1
Riparian open woodlands—island banks	12.1
Riparian dense woodlands—mainland banks	38.6
Riparian dense woodlands—island banks	29.5
Celtis woods	2.1
Riparian marsh	2.0
Unvegetated bankline—mainland banks	3.3
Unvegetated bankline—island banks	0.6
Upland vegetation—mainland banks	3701.0
Upland vegetation—island banks	142.0
Upland woods, planted trees	47.5
Cropland—mainland banks	2931.5
Cropland—island banks	24.8
Farmstead—mainland banks	57.1
Farmstead—island banks	0.4
Livestock pens, corrals, etc.—mainland banks	4.6
Major roads*	1.0
Bridges/dams	1.7
Buildings	22.8
Boat landings/parking lots, etc.	12.3
Towns, urban, and residential areas	132.0
Severely impacted areas	37.2
Unknown (unclassified)	0.5
Riparian of tributary streams	15.7
Riparian of irrigation canals or returns	18.7
Tributary streams*	1.8
Irrigation canals or returns*	0.1
Lake/reservoir/pond	4.6
Nonriparian wetlands	129.0
Open river channel	1619.5
Backwater, old river channel	7.8
Shallow areas in open river channel	3.0
Sand/mudflats along mainland banks	4.5
Sand/mudflats along island banks	2.0
Sand/exposed substrate in tributary stream	0.3
Aquatic vegetation	1.0
TOTAL	9315.8

*Generally digitized as line features.

other riparian categories, rather than through colonization of bars at the river margin.

Total island area increased by 14% (37 ha) from 1938–39 to 1987 (Fig. 10). Most of this increase (76%) was due to expansion of island riparian vegetation. About 59% occurred between 1969 and 1987, with very little change between 1939 and 1957. This proportional increase was more or less equal across all 4 reaches. Islands that became attached to main banks during the time series were excluded from the above analyses.

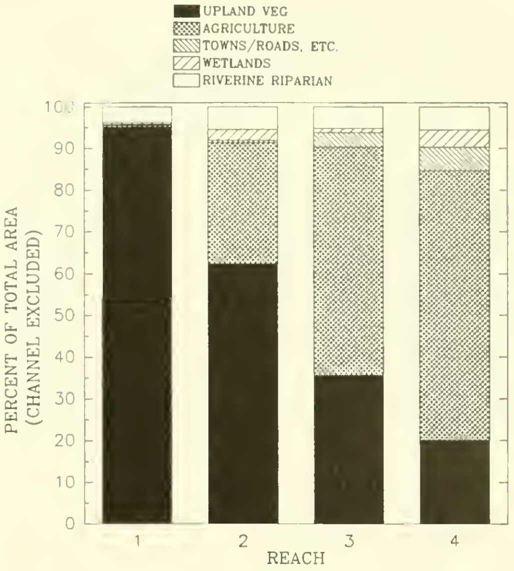

Fig. 6. Proportion of land cover types across different reaches of the study area from 1987 aerial photographs.

DISCUSSION

Vertical zonation of vegetation communities reflects individualistic responses of species and lifeform groups to underlying gradients of decreasing scouring and flood disturbance, decreasing frequency and length of inundation, and decreasing soil moisture (or increasing depth to water table) from the water's edge to the top of the bank profile (Johnson et al. 1987, Auble et al. 1994). Elevation above water surface serves as a surrogate variable that integrates these underlying gradients. On the middle Snake River, lower-elevation zones are dominated by species tolerant of frequent inundation and by ruderal, annual species. At progressively higher elevations above mean water surface, larger, longer-lived lifeforms of vegetation predominate—first perennial forbs and shrubs (shrub-forb zone) and then trees. Vegetation reverts to herbaceous perennial and annual species and shrubs at higher elevations (transitional grass-shrub and upland shrub zones) as water becomes more limiting.

Vertical zonation patterns were affected by seepage and anthropogenic disturbance. Both were ubiquitous in downstream sections of the study area. Seepage, in particular, changed the patterning of vegetation, providing habitat for seep-specialist species, obscuring the typical

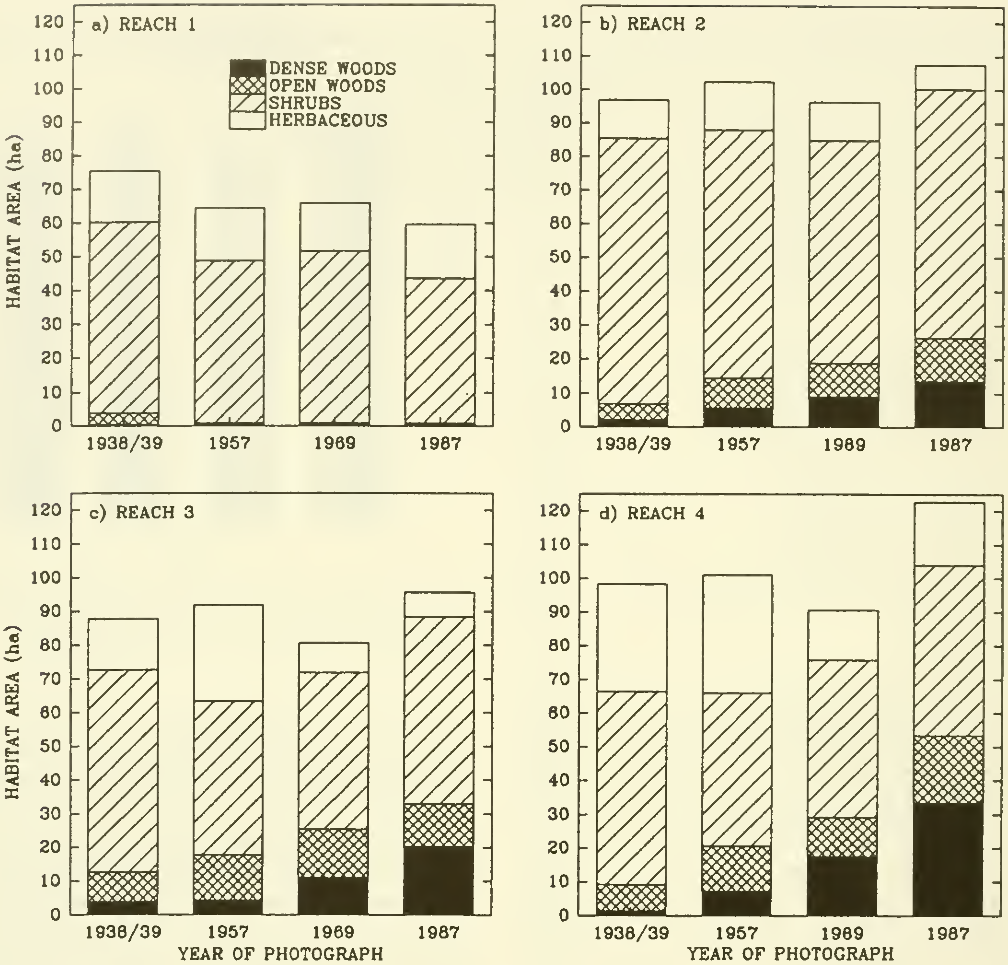

Fig. 7. Coverage of riparian habitats (excluding *Celtis* woodland) by reach across the time series of aerial photographs.

vertical moisture gradient, and supplying nutrients. Seeps were extremely variable, based on the location at which moisture emerged in the hillside and the amount of flow, and thus did not produce apparent zonation patterns. Most seepage was probably from leakage of irrigation canals or from elevated local water tables due to irrigation, thus adding both moisture and nutrients to the riparian community. Consequently, the incidence of seepage was greatest in downstream sections of the study area where agriculture is the dominant land use.

The extent of riparian woodland in presettlement and prewater development times was not investigated. We have determined, however, that riparian woodland has increased considerably in the middle Snake River since the late 1930s. The increase in woodland area, especially large on islands, was accompanied by an overall increase in island and total riparian habitat as well as island area. Largest increases in total riparian and island area occurred between 1969 and 1987.

Several factors, alone or in concert, may be responsible for these increases: declines in minimum flows since the 1950s, possible declines in peak flows since the 1920s, planting and naturalization of exotic tree species, and sediment inputs from intensive agriculture. Increased woodland suggests that changes in the flow regime enabled expansion of the riparian zone and increased the suitability of islands and mainland banks for tree establishment. Although historic changes in the hydrograph have been

TABLE 8. Accuracy of photo interpretation of the major cover categories, from results of field checks of GIS maps (see Johnson et al. 1995 for methodology). $\hat{K}$ represents an estimate of classification accuracy, corrected for chance agreement (Campbell 1987).

Cover category*	Total # polygons	Total # correct	% correct
Riparian herbaceous	38	32	84.2
Riparian shrub	71	64	90.1
Riparian open woods	12	9	75.0
Riparian dense woods	5	3	60.0
Cropland	33	33	100.0
Upland	35	31	88.6
Wetlands	16	14	87.5
Upland trees	12	12	100.0
Stream riparian	7	7	100.0
TOTAL RIPARIAN	126	108	85.7 $\hat{K}$ = 74.8
TOTAL (ALL CATEGORIES)	248	223	89.9 $\hat{K}$ = 88.0

*Several minor categories are not shown.

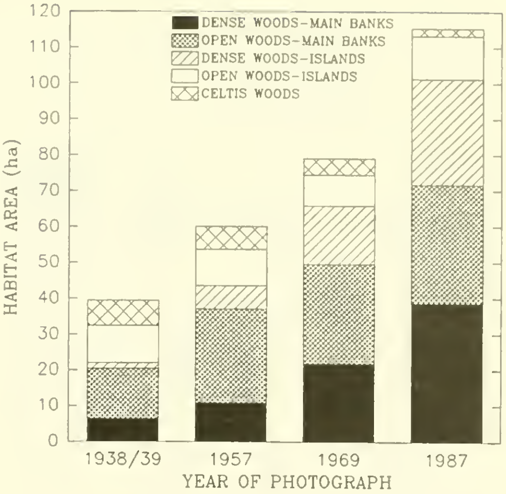

Fig. 8. Changes in area of riparian woodlands on island and main banks in the study area across the time series of aerial photographs.

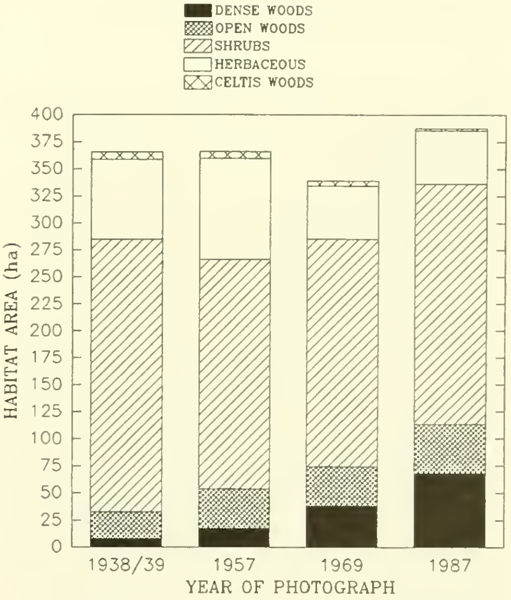

Fig. 9. Changes in area of riparian habitats in the study area across the time series of aerial photographs.

relatively minor, there has been a significant decrease in minimum annual flow since the 1950s. With reduced minimum flows, river margins have become exposed for longer periods during the growing season, leading to expansion of riparian vegetation and downslope shifting of vegetation zones (Johnson 1994, Johnson et al. 1995). Thus, lower minimum flows may have led to vegetation establishment on previously unvegetated surfaces in the channel, increased island and riparian area, and eventually (with succession) to mature woodland.

Reduced peak flows also may be a factor. Annual peak flows in the first 13 yr of record (1914–1926) averaged significantly higher than those after completion of American Falls and Palisades dams. However, comparisons are difficult because there is no hydrograph record prior to construction of older dams such as Swan Falls. Reduction of peak flows may have reduced the erosiveness of the river, allowing expansion of woody vegetation (Johnson 1991, 1994).

The introduction and spread of exotic tree species also may have contributed to woodland expansion in the Snake River system. *Tamarix* and *Elaeagnus* have become well established in the western United States since the 1930s (Christensen 1962, 1963). In some areas of the West, *Tamarix* has been an aggressive invader (Brotherson and Field 1987, Brock 1994) that has outcompeted native species and occasionally caused system-wide changes in channel morphology (Graf 1978, Nadler and Schumm 1981, Blackburn et al. 1982). On the middle Snake neither of these species appears

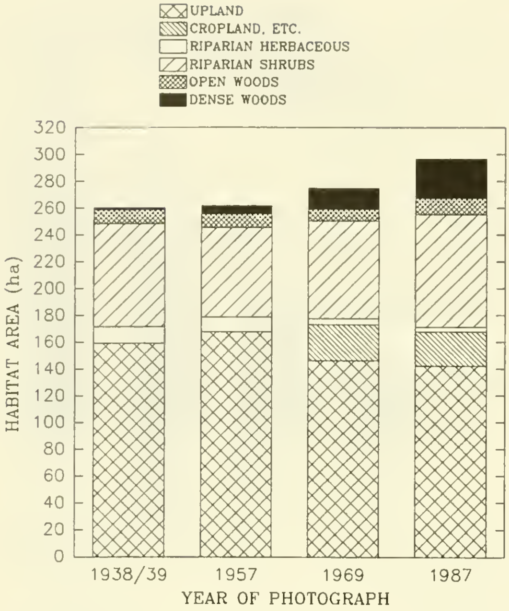

Fig. 10. Changes in area of island habitats in the study area across the time series of aerial photographs.

to be an aggressive, system-altering invader, but both have probably benefited from the effects of anthropogenic disturbance such as salinization from irrigation seepage, moisture amendments from irrigation, burning or clearing of the riparian zone, and cattle grazing (Carman and Brotherson 1982, Brotherson and Field 1987).

In the contemporary river approximately 2/3 of the trees are exotic species, principally *Elaeagnus* and *Tamarix*. These species not only may be more tolerant of anthropogenic disturbance (grazing, burning, etc.) and possess different regeneration niches than *Salix* (Irvine and West 1979, Howe and Knopf 1991, Shafroth et al. 1995), but also may occur slightly higher in the riparian zone than do the native willows (Knopf and Olson 1984). Increases in irrigation and anthropogenic disturbance may have particularly benefited *Elaeagnus*, which does not depend on depositional habitat near the river for regeneration as *Salix* does. The native *Salix* woodlands probably have increased in area also, since they currently make up nearly half of the trees in reach 4.

The paucity of trees and exotic herbaceous plants (*Lythrum*) in reach 1 may be related to the relatively steep stream gradient and to sequestering of fine sediments by Swan Falls Dam, leaving little sediment for bar formation and aggradation during floods. Also, large variation in river stage in reach 1 caused by the power generation schedule and the V-shaped channel may inhibit plant establishment. *Celtis* woodlands in this reach occur at a high bank gradient position, suggesting some independence from riverine influences (DeBolt and McCune 1995).

Downstream the river flattens out and widens, coverage by intensive agriculture increases, and bed material becomes finer. The sediment sequestering effect of dams attenuates with distance downstream (Williams and Wolman 1984), and fine sediments are added downstream by tributary streams and irrigation returns. Because of this, downstream reaches (especially reach 4) may provide a better recruitment environment for seedlings of riparian trees as well as for purple loosestrife. In addition, more trees have been planted in the vicinity of human settlement downstream, increasing local populations and seed sources of exotic species like *Elaeagnus*, *Tamarix*, and *Ulmus*.

The proliferation of purple loosestrife in the 1990s could have significant future consequences for vegetation-channel dynamics. In wetlands in the eastern United States, loosestrife is an aggressive invader that crowds out native species and degrades wildlife habitat (Thompson et al. 1987). Our observations suggest that loosestrife is widespread, spreading, and prolifically colonizing gravel bars under low flow conditions on the middle Snake. Seeps may provide the reservoir of propagules for colonization during these recruitment windows, offering wet, high-nutrient conditions that enable loosestrife to flourish locally until prolonged low flows expose available substrate. Unlike many native species colonizing gravel bars, loosestrife is a tall perennial, grows in monospecific stands, reproduces vegetatively or by seed, and can withstand significant flood training and inundation by flowing water. These characteristics may enable loosestrife to persist better than native annual species on gravel bars, perhaps leading to enhanced sediment trapping by vegetation and eventual bar aggradation and stabilization. The effects of such a new species to the system could lead to further riparian zone expansion and perhaps even closure of small, shallow channels. This would be of special concern along the middle Snake because of the possible land-bridging of islands that serve as waterfowl nesting areas (Johnson et al. 1995). The influence of purple loosestrife on channel dynamics and geomorphology in riverine systems deserves close monitoring and further study.

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TEMPORAL PATTERNS OF SEEDLING EMERGENCE AND EARLY SURVIVAL OF GREAT BASIN PERENNIAL PLANT SPECIES

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ABSTRACT.—We seeded *Agropyron cristatum* and 16 native Great Basin perennial species on *Bromus tectorum*–dominated sites to compare temporal patterns of seedling emergence and early survival among species. To indicate variability between sites and between years, plots were planted on 2 sites in western Utah in autumn 1994, and plantings were repeated near 1 site in autumn 1995. Two sites included burned and unburned seedbed treatments. We monitored seedling emergence and survival from early winter until July of the 1st year. Four seasonal patterns of emergence were evident, indicating considerable potential for different seasonal patterns of precipitation to favor recruitment of different species. Emergence of all shrubs, except *Ephedra nevadensis*, began in February and essentially ended by April. Seedlings of *Ephedra nevadensis* and of the grasses *Agropyron* and *Pseudoroegneria spicata* emerged over an extended period from February through June. Most other grasses and the 2 forbs began emerging in April and continued into June. *Pleuraphis jamesii* emergence did not begin until May. Although many seedlings of the 3 chenopod shrubs emerged, none survived, suggesting their episodic recruitment is more a function of survival than of emergence. Survival of 2 *Chrysothamnus* species was also low. *Pseudoroegneria* and *Agropyron* had the highest numbers of seedlings surviving on the moister site, followed by *Elymus elymoides* and *Stipa comata*. Survival of *Agropyron*, but not the native *Elymus*, was more depressed on the drier of the 2 sites planted in 1994. *Stipa*, *Oryzopsis hymenoides*, *Pleuraphis*, and *Ephedra* survived as well on the drier site as on the moister site, or better. On the 1995 planting site *Bromus* was greatly reduced by the burn treatment, and, in contrast to the effect of burn treatments on the 1994 site, survival of all species except *Oryzopsis* and *Ephedra* was higher on burned than on unburned treatments. Overall, *Stipa*, *Oryzopsis*, and *Pleuraphis* had low emergence but consistently high survival.

Key words: seedling emergence, seedling survival, semiarid area, Great Basin, grasses, shrubs, forbs, Bromus tectorum, *vegetation dynamics.*

Control and timing of germination are considered to be key elements in the survival of populations of plant species that reproduce primarily by seeds (Harper 1977). In arid and semiarid environments, timing of germination may be especially crucial because the amount and timing of precipitation are highly variable (Evenari 1985, Kigel 1995). In the Intermountain West, spring moisture and temperature conditions change rapidly, and narrow windows exist for emergence and establishment of perennial seedlings (Kitchen and Monsen 1994). Consequently, germination and seedling establishment of many desert and steppe perennials are rare and episodic (Ackerman 1979, Romney et al. 1980, Gutterman 1993, Kigel 1995).

Germination characteristics are important components of adaptive life history strategies of individual species (Angevine and Chabot 1979). Even within the same semiarid site, different species often possess different germination strategies (Gutterman 1993, Kigel 1995). Thus, the high variability of precipitation and temperatures typical of semiarid sites can result in conditions favoring recruitment of different species in different years. Although longer-term survival is also important, emergence and early survival play critical roles in determining recruitment of plants on semiarid sites. Emergence characteristics determine which species have seedlings initially present under what conditions, and the early period after emergence is often the time of greatest mortality. Knowledge of seasonal timing of seedling emergence and of patterns of early survival, coupled with information on the site and weather conditions under which emergence and survival occur, will aid in restoration and revegetation efforts. It is also essential in understanding natural dynamics of vegetation of semiarid sites and ultimately managing such vegetation. Community composition and dynamics may be strongly altered by periodic flushes of recruitment of particular species that occur when weather conditions favor their emergence and early survival (e.g., Westoby 1980, Neilson 1986, Westoby et al. 1989). These processes of episodic establishment of different species at different times can also lead to greater community diversity, as species established at different times accumulate on the site (Chesson 1994).

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Most Great Basin germination studies have involved laboratory experiments on dormancy and effects of temperature and photoperiod on germination, while studies of field emergence have usually dealt with only a single or a few species. Few researchers have compared patterns of emergence of a variety of species. A notable exception is Ackerman (1979), who described natural seedling emergence and survival in relation to season and weather for 11 perennial species in a Mojave–Great Basin ecotonal community. Young et al. (1994) compared recruitment of 6 native and introduced perennials in relation to precipitation on arid sites in Nevada, but timing of germination was not compared. We present a comparison of patterns of seedling emergence and early survival of 16 species native to semiarid areas of the Great Basin and 1 nonnative species planted in a single seeding experiment. To better understand the variability that occurs across different types of semiarid sites, we performed experimental seedings on 2 sites in a single year. Because conditions can differ between years, favoring different species in different years, a 3rd experiment was planted near 1 of these sites in the following, drier year. As the experimental plantings were on sites dominated by the alien annual *Bromus tectorum* (cheatgrass), inferences that we can make about emergence and early survival of these species are pertinent to reclamation on semiarid Great Basin sites. As well as removing litter and standing vegetation, fires usually greatly reduce *Bromus* seedbanks (Young and Evans 1978). Thus, we included burned and unburned seedbed treatments to test the effects of reduction of *Bromus* competition and other changes produced by fires on emergence and early survival of the seeded species.

METHODS

Study Sites

In late October–December 1994, we planted plots at 2 substantially different *Bromus*-dominated sites at the U.S. Army Dugway Proving Grounds, Tooele County, Utah, USA, with another experiment planted near 1 of the sites the following year. One site served as the main experiment site where all 17 species were planted. Subsets of these 17 species were planted in the other 2 experiments. The main experiment site, the "Hill" site, is a gently sloping area at an elevation of 1620 m at the southeastern end of the Cedar Mountains (40°16′00″N, 112°49′40″W). The 2nd site, the "Near-Dune" site, is near the base of the Cedar Mountains at 1480 m elevation (40°14′30″N, 112°50′10″W), nearly level, and about 5 km southwest of the Hill site. Mean annual precipitation for the nearest weather station, about 8 km southwest of the Near-Dune site at a slightly lower elevation in an open flat, is 20 cm (U.S. Army Dugway Proving Ground, Meteorological Operations Office). Situated at the base of Cedar Mountains and in the path of weather fronts approaching from the south and west, the Near-Dune site probably receives slightly more than this. The somewhat higher-elevation Hill site, located at the end of the Cedar Mountains range, probably receives substantially more; we observed it to receive more snow in winter. The following autumn (December 1995) we planted another site, the "Dune-Area" site, about 0.5 km from and at approximately the same elevation as the Near-Dune site. The 1st year was unusually wet, with 29.4 cm of precipitation from October 1994 through June 1995 at the weather station mentioned, but the 2nd year was considerably drier, with 14.3 cm from October 1995 through June 1996.

A partial analysis and description of soils of the 3 sites was done so we could identify ecologically meaningful soil differences among the 3 sites. Soil texture was determined by feel. Mean sand size was estimated using a dissecting microscope and digital calipers. Water-soluble cations were determined by atomic absorption spectrophotometry of saturation paste extracts, and nitrate nitrogen and available phosphorus were determined. Soil texture and particle size analyses were provided by J.L. Boettinger of the Plants, Soils and Biometeorology Department, Utah State University, Logan, Utah. Nitrogen, phosphorus, and cation data were provided by the Analytical Labs, Utah State University.

Soils of the 3 sites were similar in most respects. All 3 sites had deep soils (>1.5 m) derived from eolian deposits. All 3 soils were

TABLE 1. Soil texture, nitrate-nitrogen, phosphorus, and cation concentrations for the 3 sites. Texture information refers to the upper 75 cm, as textures for a particular site did not differ within this depth interval. Estimated available water-holding capacity is based on texture alone and is expressed as cm of water/cm of soil (USDA Soil Conservation Service 1967).

Site	Texture class	Sand (%)	Mean sand size (mm)	NO_3–N	P	Na	Ca	Mg	K	Water-holding capacity (cm/cm)
				|------mg/kg------|		|------------------mg/L------------------|				
Hill	Loamy fine sand	85	0.12	2.6	7.3	18.5	12.7	6.3	52.0	0.09
Near-Dune	Fine sand	90	0.20	1.4	9.3	20.8	39.3	5.4	37.0	0.07
Dune-Area	Sand	95	0.30	2.2	8.3	25.8	44.4	7.8	63.0	0.06

very low in nitrogen and phosphorus but high in calcium and potassium (Table 1). Concentrations of sodium were also substantial, but salinity was well below problem levels. The greatest difference among sites was soil texture. Soils of all 3 sites were dominated by sand-size particles. Soil of the Hill site had the lowest percentage of sand and smallest mean sand size (Table 1). The Dune-Area site had the highest percentage of sand and largest mean sand size. The Near-Dune site had percent sand and mean sand size intermediate between the other 2 sites. All 3 soils were sandy enough to allow rapid to very rapid infiltration (J.L. Boettinger personal communication). Of these 3 sites, the finer-textured soil of the Hill site has greater estimated available water-holding capacity. As with infiltration, all soils are sandy enough that little available water would be lost by evaporation once the soil surfaces dry out (J.L. Boettinger personal communication). Thus, though differences are minor, we interpret the soils of the Hill site to be least droughty and those of the Dune-Area site to be most droughty. Considering the greater precipitation as well as the somewhat less droughty soils, the Hill site should have substantially more favorable moisture conditions than the Near-Dune site. As the Dune-Area site was planted in a much drier year, it had still less favorable moisture conditions than the Near-Dune site.

Experiments

We planted 1 nonnative species commonly used in rangeland seedings, *Agropyron cristatum* (crested wheatgrass), and 16 native perennial grasses, shrubs, and forbs occurring on or near the sites (Table 2). Seeding rates (Table 2) were based on recommendations of pounds of pure live seeds per acre by Vallentine (1989) and by Granite Seed Co., Lehi, Utah. All seeds were commercially obtained from Granite Seed Co. except *Grayia spinosa* and *Oenothera pallida*, which were from Comstock Seed Co., Reno, Nevada. (After their first mention in the text, we refer to species by genus name only except for *Chrysothamnus*, which was represented by more than 1 species.) Our gross seeding rates were adjusted to obtain the desired amount of pure live seed per unit area using percent pure live seed listed by the commercial providers for our seed lots.

The design of the main experiment, located at the Hill site, consisted of 2 blocked replicates, each with a burned and an unburned macroplot (i.e., a split-plot design with respect to burn treatment within each of the 2 blocks). Within each macroplot we delineated 68 individual 3 × 3-m plots, each planted with 1 of the 17 species at 1 of 4 depths (surface, or simulated drilling at 1 cm, 2 cm, or 3 cm). Each plot contained 10 planted rows 30 cm apart. Rows within plots were treated as subsamples in the analyses. Burned and unburned macroplots were paired approximately 20 m apart on each side of the border of a wildfire that burned in a *Bromus*-dominated community the previous July. The burn border location was not related to site or vegetation characteristics; the fire was advancing slowly in this direction and fire fighters extinguished it at this particular location.

Designs of the other 2 experiments were modified from that of the main experiment. The Near-Dune site did not include a burn

TABLE 2. Species planted and seeding rates. Grasses are listed by tribe and other species by family. Tribes of grasses are from Gould (1968). Nomenclature of Triticeae is from Barkworth and Dewy (1985). Otherwise, nomenclature is from Welsh et al. (1987). Seeds/m^2 are based on recommendations of pounds/acre of pure live seeds and estimates (listed by the commercial seed providers) of percent pure live seed for the seed lots we used. Seeds/3-m row are based on seeds/m^2 and number of rows/m (but are adjusted in some cases; e.g., for *Agropyron*, we used the same seeding rate/row as for most other Triticeae). For species for which recommendations were not available, we used recommended seeding rates for similar species. All species listed were planted on the Hill site. Species that were also planted on the Near-Dune and Dune-Area sites are indicated by +.

Species	Seeds/m^2	Seeds/3-m row	Near-Dune	Dune-Area
Grasses				
TRITICEAE				
Agropyron cristatum	490	200	+	
Pseudoroegneria spicata	210	200		+
Elymus elymoides	430	300	+	+
Pascopyrum smithii	210	200		+
STIPEAE				
Oryzopsis hymenoides	210	200	+	+
Stipa comata	230	200	+	
CHLORIDEAE				
Pleuraphis jamesii	240	300	+	+
ERAGROSTEAE				
Sporobolus cryptandrus	370	300	+	
Shrubs				
ASTERACEAE				
Artemisia tridentata	440	400	+	
Chrysothamnus nauseosus	—	300		+
C. viscidiflorus	—	300	+	+
CHENOPODEACEAE				
Atriplex canescens	110	200	+	
Grayia spinosa	300	200	+	
Sarcobatus vermiculatus	—	200	+	
EPHEDRACEAE				
Ephedra nevadensis	—	150	+	+
Forbs				
MALVACEAE				
Sphaeralcea munroana	490	400	+	
ONAGRACEAE				
Oenothera pallida	630	500	+	

treatment. It also differed in that only surface and 2-cm planting depths were used, and only 14 of 17 species planted on the Hill site were planted: 2 species were omitted because they did not occur near the site, and 1 *Chrysothamnus* species was omitted (Table 2). On the Dune-Area site we planted 8 species that showed promise based on the 2 experiments planted in the 1st year (Table 2). Also, based on results of the 1st year, only simulated drilling at 2-cm depth was used. The Dune-Area experiment further differed in that plots were smaller: 2.5 × 2.5 m with 7 rows planted 30 cm apart. As on the Hill site, the Dune-Area experiment included a burn treatment with the burned macroplots located on a wildfire, but in this case a dirt road created the border between burned and unburned macroplots.

We planted by simulated drilling using a curved metal plate in a wood frame. The plate, after being adjusted to 1-cm, 2-cm, or 3-cm depth, was used to cut grooves for planting. We dropped seeds into grooves by hand, after which we heavily raked over the rows to close the grooves. Surface seeding was done in rows about 10 cm wide which were then raked over. For species whose individual seeds were difficult to identify because the commercially supplied seeds were mixed with fragments of inflorescences (*Artemisia tridentata*, *Chrysothamnus nauseosus*, *C. viscidiflorus*), and species with very small seeds (*Sporobolus cryptandrus*, *Oenothera*, *Sphaeralcea munroana*), we used weighed portions of seeds corresponding to the desired number of seeds per row.

In the first 2 experiments (Hill and Near-Dune), emergence of some species began during a warm period in February. In a 1st census to quantify this early emergence, we simply counted seedlings per row on 20–26 February. In 2 following censuses we mapped locations of seedlings along rows using a 3-m ruler laid along the row. If seedlings were relatively sparse, 8 of the 10 rows per plot were mapped, excluding 1st and last. If seedlings were very dense (>50/row), only 4 rows were mapped, excluding the 4 central rows, as well as 1st and 10th. We conducted the 2nd census, in which seedlings were first mapped, for the 1st replicate (block) of both sites on 29 March–29 April 1995 and censused the 2nd replicate on 30 April–19 May (weather intermittently prevented fieldwork). The 3rd census, in which we relocated seedlings using these maps to determine seedling survival and mapped newly emerged seedlings, occurred 27 June–3 July and 8–19 July for replicates (blocks) 1 and 2, respectively. Because emergence of *Pleuraphis jamesii* and *Sporobolus* occurred much later than that of the other species and none were found in earlier censuses, we first mapped seedlings of these 2 species on 17–22 June and recensused them on 10–20 July. On the Dune-Area site planted in the 2nd year, emergence was censused in mid-February but found to be very low. The initial seedling mapping was done 21–31 March 1996, with a 2nd mapping census 28–31 May. Survival was censused 29 June–2 July. *Pleuraphis* was included in the May and June–July censuses.

On the Hill and Near-Dune sites, we calculated survival as the proportion of seedlings recorded in the April census (the 1st mapping) that were alive in the June–July census. For later-emerging *Pleuraphis* and *Sporobolus*, survival was the proportion of seedlings recorded in June that were alive in the July census. For the Dune-Area site, survival was the proportion of all seedlings recorded as emerging in either the late March or May censuses that were alive in the June–July census.

Analyses

We analyzed emergence and survival until July by analysis of variance (ANOVA). The response data consisted of emergence or proportional survival per row with rows constituting subsamples within plots. In addition to the analyses of proportional survival, we also ran ANOVAs with number of seedlings surviving as the response, so that we could make some individual comparisons of the actual numbers of seedlings recruited in the 1st growing season. All ANOVA analyses were done with the GLM Procedure (SAS 1990). Univariate and Frequency Procedures (SAS 1990) were used to verify that data distributions did not differ greatly from a normal distribution. We used the Frequency Procedure for this purpose, in addition to the Univariate Procedure, because a "heavy tailed" distribution with many zeros was the predominant way data sets differed from a normal distribution, and this procedure more clearly identified this problem. Arcsin square root transformations were used on proportional survival data and yielded acceptable data distributions. Natural log transformations were used on emergence data. Square root transformations were used on number of seedlings surviving. We analyzed emergence separately for each sampling period that had sufficient emergence. Data sets for some time periods with very low emergence had many zeros, violating the assumptions of ANOVA. For this reason emergence was not analyzed for the last emergence sampling period for each site nor for the February sampling periods on the Near-Dune and Dune-Area sites. When 2 time periods per site were analyzed (Hill site), they were analyzed separately; thus, repeated-measures ANOVA was not used. Species with a mean of <1 seedling per plot were omitted in all ANOVAs.

We made statistical comparisons between the 2 sites planted the same year (Hill and Near-Dune sites) using the subset of data from the Hill site that conformed to the reduced experimental design of the Near-Dune site (see above): data from unburned macroplots and the 2-cm planting depth for the 14 species shared between the 2 sites. A statistical comparison of the 2 experiments on very similar sites planted in different years (Near-Dune and Dune-Area) was not done because the 2 sites had only 5 species in common, some of which had insufficient emergence for analysis. Instead, we statistically compared the Hill and Dune-Area sites, i.e., a comparison across years and sites, including burn treatments nested within site. This provided a much more extensive comparison than comparing the Near-Dune and Dune-Area sites because both sites had burn treatments and more species were shared between the 2 sites. Furthermore, since the Dune-Area site is a lower-elevation site planted in the drier year, this comparison is of interest because it compares sites with the most favorable and least favorable moisture conditions.

RESULTS

Preliminary to the other analyses, we conducted an initial analysis of emergence on the Hill site for the April census when most emergence occurred, with depth included as a factor. In this analysis the Species × Burn × Depth interaction was significant ($F = 18.1$, df $= 84$, $P < 0.001$). The major effects responsible for this 3-way interaction were that, of all species, only the 2 *Chrysothamnus* species had substantial emergence on surface-seeded plots, and their emergence on surface plots was much higher on burned than unburned seedbed treatments. Even the *Chrysothamnus* species had reduced emergence with surface seeding relative to the 3 drilling depths, however. Emergence was generally similar among the 3 simulated drilling depths, but some species (*Atriplex canescens* and *Sarcobatus vermiculatus*) had poorer emergence at 3-cm depth. Differences in emergence between planting depths were apparently reduced because plots were wet when planted, and rows subsequently dried and cracked open, reducing effective differences in planting depth.

The major difference in emergence associated with seeding depth was between surface seeding, with very low emergence, and the 3 simulated drilling depths, all with similar emergence that was considerably higher than that of surface seeding. Consistently very low emergence on surface plots greatly increased the number of zeros in the data sets, making it questionable, in some cases, whether ANOVA could be used validly for the analyses. Therefore, to provide a more statistically sound (and simpler, with the depth factor removed) ANOVA analysis, we omitted surface seeded plots and pooled the 3 drilling depths for our main analyses. As differences with seeding depth were almost entirely between surface seeding and the 3 simulated drilling depths (very few of the many paired comparisons among drilling depths were significant in this initial analysis), we considered changing our overall statistical design in this way to be valid.

Emergence

At the Hill site all shrubs and 2 grasses (*Agropyron* and *Pseudoroegneria*) began emerging in February (Fig. 1). First emergence was recorded in April for the 2 forbs and the other grasses, except for the C_4 grasses *Pleuraphis* and *Sporobolus*, which began emerging even later. Emergence was greatest on the April census for all 4 Triticeae (*Agropyron*, *Pseudoroegneria*, *Elymus*, *Pascopyrum smithii*) and for *Oryzopsis*, *Stipa*, *Ephedra*, and *Oenothera* (Fig. 1). However, the 2 *Chrysothamnus* species and the 3 chenopod shrubs (*Atriplex*, *Grayia*, *Sarcobatus*) had similar, if not higher, emergence in February versus April. Emergence of *Artemisia* was very low throughout (<0.5 seedling/row) but occurred mainly in February. No emergence for the chenopod shrubs and very little for *Chrysothamnus* occurred after April (Fig. 1). All other species had emergence through June. *Agropyron*, *Pseudoroegneria*, and *Ephedra* had the most extended period of emergence, from February through June (Fig. 1). *Pleuraphis* emergence continued into July.

Mean comparisons we present throughout (e.g., comparisons between species or comparisons of the same species between 2 sites) were done by *t*-test comparisons of LSMeans (least squares estimates of marginal means for unbalanced designs). Because several of these mean comparisons per ANOVA were often used, chances of incorrectly rejecting a null hypothesis in at least 1 of the comparisons may be somewhat higher than the *P*-values indicate. Therefore, we used the customary 0.05 probability level as the cutoff for declaring means significantly different, but we note those means that were more marginally significant ($0.01 < P < 0.05$) by individually stating those *P*-values. Thus, unless otherwise stated, all means declared significantly different had $P < 0.01$.

In the Hill site analyses with surface-seeded plots omitted and other depths pooled, the Species × Burn interaction was significant for both February and April emergence ($F = 5.5$, df $= 9$, $P < 0.001$; $F = 13.3$, df$=14$, $P < 0.001$; respectively), indicating species responded differently to burn treatment. In February, *Atriplex* ($P < 0.05$) and the 2 *Chrysothamnus* species had significantly higher emergence on burned than unburned plots. In April, *C. nauseosus* continued to have higher emergence on burned plots, along with *Oenothera*, *Agropyron*,

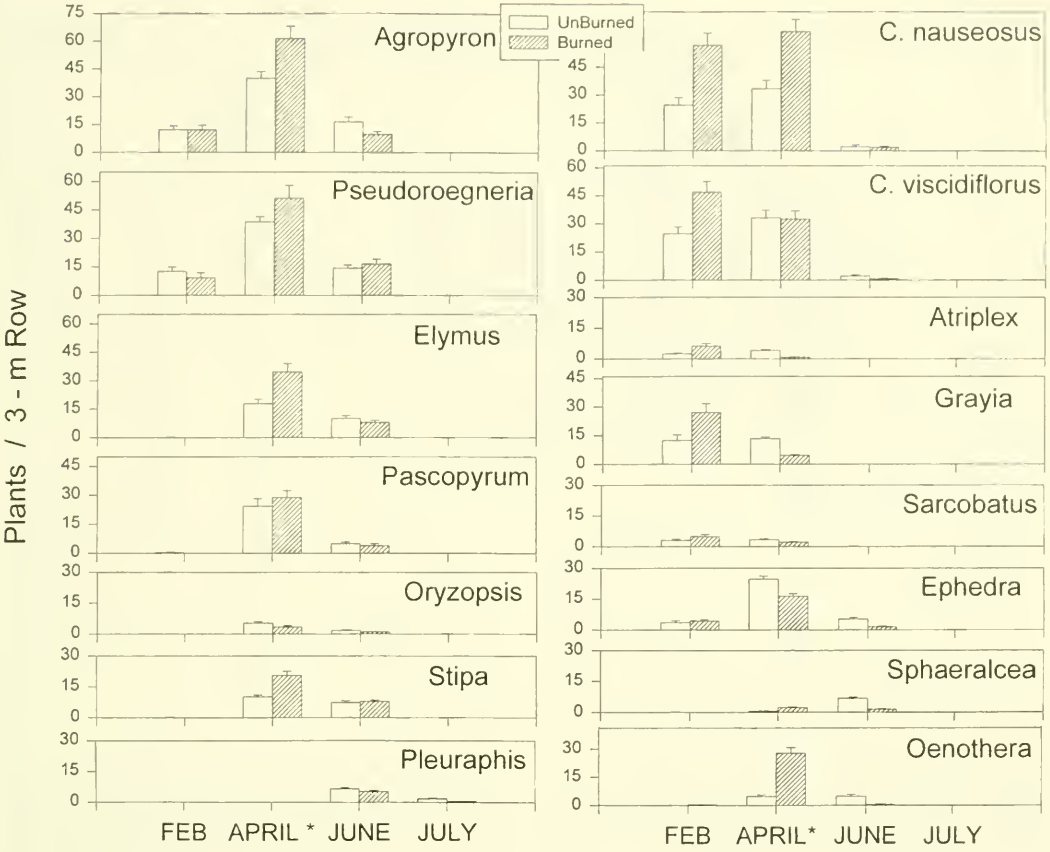

Fig. 1. Seedling emergence on unburned and burned plots on the Hill site (excluding *Artemisia* and *Sporobolus* which had extremely low emergence at any time). For each species and burn treatment at each sampling period, mean emergence/3-m row and standard errors for the 3 simulated drilling depths combined are presented. *Emergence shown for April actually includes plants surviving from February emergence, as February's seedlings were not individually marked.

Elymus, and *Stipa*. In contrast, *Atriplex*, *Grayia*, and *Ephedra* had significantly more emergence on unburned than on burned plots in April.

In the comparison of April emergence between Hill and Near-Dune sites, the Species × Sites interaction was significant ($F = 5.1$, df = 10, $P < 0.001$). *Oryzopsis*, *Stipa*, *Sphaeralcea*, *Atriplex*, and *Oenothera* had significantly more emergence on the Near-Dune site than on the Hill site (Fig. 2). Emergence of *Agropyron* and *Elymus* was less distributed over time on the Near-Dune site than on the Hill site (Fig. 2).

On the Dune-Area site, the Species × Burn interaction was again significant ($F = 2.6$, df = 6, $P < 0.05$). In the comparison of emergence between the Dune-Area and Hill sites (April census on the Hill site and March census on the Dune-Area site, with data from the smaller Dune-Area plots standardized to emergence per 3-m row), the Species × Burn (within Sites) and Species × Site interactions were significant ($F = 3.8$, df = 12, $P < 0.001$; $F = 20.6$, df = 6, $P < 0.001$; respectively). On the Dune-Area site, *Pseudoroegneria*, *Pascopyrum*, *C. nauseosus*, and *C. viscidiflorus* had significantly higher emergence on unburned than on burned plots (Fig. 3), whereas on the Hill site emergence was similar on burned and unburned plots for all these species except *C. nauseosus*, which had higher emergence on burned plots. *Elymus*, with its similar emergence on burned and unburned plots on the Dune-Area site, also had higher emergence on burned plots on the Hill site. Emergence of the 2 *Chrysothamnus* species on the Dune-Area site also differed from the other 2 sites in that only a few seedlings emerged in February, and emergence was lower overall (Fig. 3).

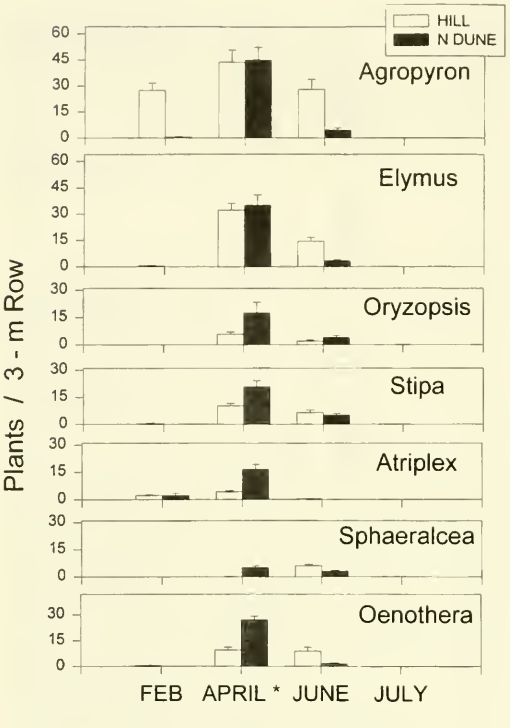

Fig. 2. Seedling emergence on the Hill site and the Near-Dune site for those species that differed between sites (the other species on the Near-Dune site were *Pleuraphis, C. viscidiflorus, Grayia, Sarcobatus,* and *Ephedra*). For each species at each sampling period on each site, mean emergence/3-m row and standard errors for the 2-cm simulated drilling depth plots are presented. (*See Fig. 1.)

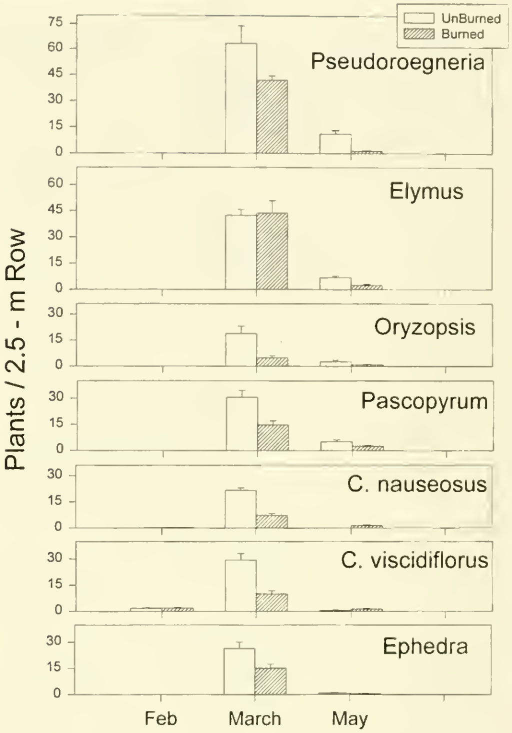

Fig. 3. Seedling emergence on unburned and burned plots on the Dune-Area site planted in the 2nd year (excluding *Pleuraphis* which had no emergence). For each species and burn treatment at each sampling period, mean emergence/2.5-m row and standard errors are presented.

Emergence of *Ephedra* was concentrated in March (Fig. 3) rather than distributed from early to late spring as on the other sites in the wetter year. *Pleuraphis* had no emergence in this drier year. *Pseudoroegneria* had no February emergence on the Dune-Area site. Thus, both *Pseudoroegneria* on this site and *Agropyron* on the Near-Dune site lacked February emergence on the lower-elevation sites where they were planted.

Proportion of Seedlings Surviving

The Species × Burn interaction for the Hill site was significant ($F = 3.1$, df = 10, $P < 0.001$). Survival of the 3 chenopod shrubs was nearly zero by July, and survival of *Oenothera* and the 2 *Chrysothamnus* species was low (Fig. 4). Survival until July was good for *Agropyron*, *Pseudoroegneria*, and *Elymus*, but that of *Pascopyrum*, the other Triticeae species, was lower (Fig. 4). Of the shrubs, only *Ephedra* had good survival, especially on unburned plots where its survival was significantly higher than on burned plots. *Oryzopsis* and *Stipa* had the highest proportion of seedlings surviving, along with *Pleuraphis* on unburned plots, where its survival was significantly higher than on burned plots (Fig. 4). Survival of *C. viscidiflorus* was somewhat higher on unburned than on burned plots ($P < 0.05$). No species had higher survival on burned than on unburned plots.

The Species × Site interaction in the comparison between Hill and Near-Dune sites was significant ($F = 6.0$, df = 7, $P < 0.001$). On both sites survival of the chenopods, *Chrysothamnus* species, and *Oenothera* was very low. The Triticeae planted on the Near-Dune site, *Agropyron* and *Elymus*, tended to have lower survival than on the Hill site, but only *Agropyron* significantly so ($P < 0.05$; Fig. 5). In contrast, *Oryzopsis*, *Stipa*, *Pleuraphis*, and *Ephedra* tended to have higher survival

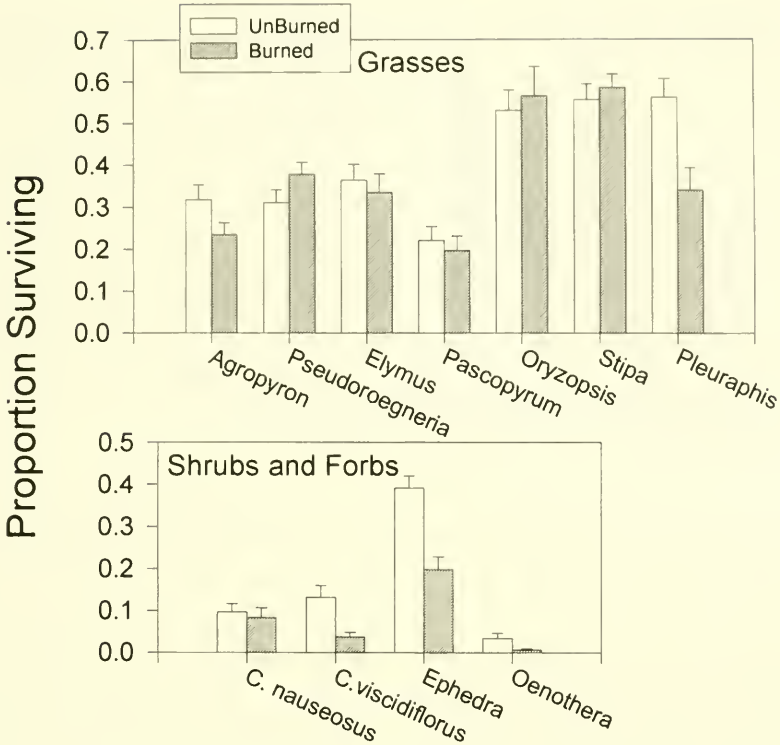

Fig. 4. Proportion of seedlings surviving until the 1st July after emergence on unburned and burned plots on the Hill site for species with enough seedling emergence to assess survival (chenopod shrubs, with considerable emergence but zero survival, are also omitted). For each species and burn treatment, mean proportion surviving/3-m row and standard errors for the 3 simulated drilling depths combined are presented.

on the Near-Dune than Hill site, but only *Stipa* significantly so.

On the Dune-Area site, the Species × Burn interaction was significant ($F = 5.9$, df = 6, $P < 0.001$). In comparing the Hill and Dune-Area sites, the Species × Burn (within Sites) and Species × Site interactions were significant ($F = 5.8$, df = 12, $P < 0.001$; $F = 6.4$, df = 6, $P < 0.001$; respectively). Survival of the 3 Triticeae on unburned plots was lower on this site in the drier year than on the Hill site in the wetter year. The burn at the Dune-Area site was more intense and reduced *Bromus* density much more than the burn on the Hill site, and survival on the Dune-Area site was much greater overall on burned than unburned plots: all species except *Ephedra* and *Oryzopsis* had significantly higher survival on burned than on unburned plots (Fig. 6). In contrast, on the Hill site survival was similar on burned and unburned plots, except for *Pleuraphis* and *Ephedra*, which had higher survival on unburned plots. *Chrysothamnus* survival was very low on unburned plots of the Dune-Area site, but on burned plots it was similar to its best survival on other sites, e.g., unburned plots on the Hill site. Similarly, survival of *Ephedra* on burned plots of the Dune-Area site was comparable to its survival on the moister Hill site in a wetter year. Only *Oryzopsis*, *Ephedra*, and *Pseudoroegneria* had substantial survival on unburned Dune-Area plots (Fig. 6).

Number of Seedlings Surviving

As with survival and emergence, Species × Burn interactions on both the Hill and Dune-Area sites, the Species × Site interaction in the comparison between the Hill and Near-Dune sites, and Species × Burn (within Sites) and Species × Site interactions in the comparison between the Hill and Dune-Area sites were all highly significant ($P < 0.001$ for all; $F = 6.9$,

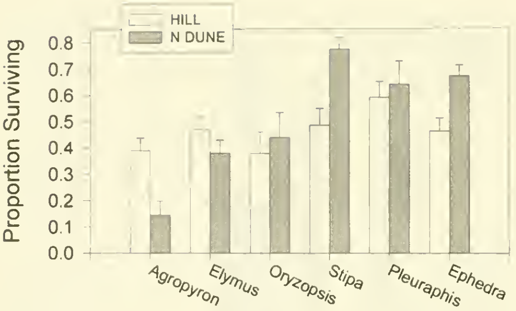

Fig. 5. Proportion of seedlings surviving until the 1st July after emergence on the Hill site and the Near-Dune site for each species that differed between sites. For each species on each site, mean proportion surviving/3-m row and standard errors for the 2-cm simulated drilling depth plots are presented.

df = 10; F = 10.1, df = 6; F = 10.0, df = 7; F = 5.8, df = 12; F = 11.4, df = 6; respectively).

On the Hill site high emergence and good survival combined to give *Pseudoroegneria* and *Agropyron* the highest numbers of seedlings surviving overall (Fig. 7). Marginally more *Pseudoroegneria* than *Agropyron* survived until July ($P < 0.05$). *Elymus* and *Stipa* on burned plots and *Ephedra* on unburned plots had numbers surviving similar to those of *Agropyron* (Fig. 7). For *Stipa*, which had low emergence, this was due mainly to high survival. Numbers of *Pascopyrum* and *C. nauseosus* surviving were significantly lower than those of *Agropyron*. *Oryzopsis*, *Pleuraphis*, and *C. viscidiflorus* were the only other species with substantial numbers surviving.

On the drier Near-Dune site, *Agropyron* seedlings surviving were about half those of the Hill site (6.1/row) due to lower survival. Significantly more seedlings of *Oryzopsis*, *Stipa*, and *Ephedra* (9.8, 15.1, and 24.2/row, respectively) survived on the Near-Dune site than on the Hill site as a result of both higher emergence and survival. The 2 of these 3 species used on the Dune-Area site, *Oryzopsis* and *Ephedra*, had the highest numbers of seedlings surviving on the apparently more stressful unburned plots in this drier year, with 8.0 (*Oryzopsis*) and 2.9 (*Ephedra*) seedlings per 3-m row. Although a high proportion of *Chrysothamnus* seedlings survived on the burned Dune-Area plots, numbers surviving were still very low because of low emergence.

A wildfire burned both the Hill and Near-Dune sites late in the 1st summer following seedling emergence, and only grasses survived this fire. On the Hill site there was some survival of all 7 grass species. Proportional survival of *Stipa* and *Pleuraphis* through the 2nd growing season following the fire was >0.05 of the recorded emergence, but survival of the other species was mostly well under 0.01. On the Near-Dune site, only *Stipa* and *Pleuraphis* survived the fire, and only *Pleuraphis* had >0.05 proportional survival. It is unknown what this later survival would have been without the wildfire.

DISCUSSION

Seasonal Patterns

Based on results of the Hill and Near-Dune site experiments, we identified 4 relatively distinct seasonal patterns of emergence. In the 2 *Chrysothamnus* species, chenopod shrubs, and *Artemisia*, emergence began very early and ended early. Winter snowcover is important to *Artemisia* recruitment, as seedling emergence occurs immediately after spring snowmelt (Meyer and Monsen 1990, Meyer 1994). Although our emergence of *Artemisia* was very limited, it occurred very early. Similarly, other reports of field emergence and laboratory studies (Meyer et al. 1989) are consistent with our early spring emergence of *Chrysothamnus*. *Grayia* is also capable of very rapid germination (Wood et al. 1976), and in the Great Basin, after seeds have experienced a cool, moist period, they can emerge in early spring (e.g., February to early March) when soil and air temperatures are still near freezing (Shaw and Haferkamp 1994). *Sarcobatus* also germinates rapidly at cool temperatures (optimal germination at 4–10° C; Eddleman 1979).

Emergence and early seedling survival of *Grayia* are very dependent on precipitation, and establishment is episodic, occurring only in years with above-average precipitation (Shaw and Haferkamp 1994). Similarly, only episodic establishment of seeded *Atriplex* has been reported (Stevens and Van Epps 1984). In our experiment many seedlings of *Atriplex*, *Grayia*, and *Sarcobatus* emerged very early, even on the drier Near-Dune site, but were very short lived. This supports the premise that winter snow and early spring soil moisture are important to these shrubs, but suggests that

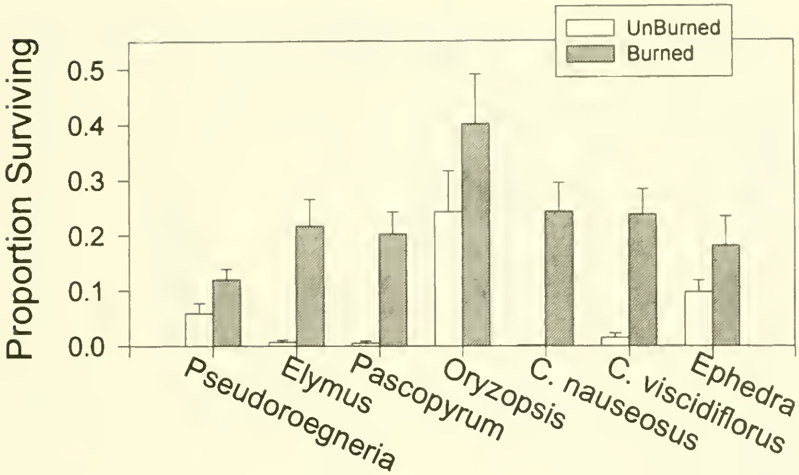

Fig. 6. Proportion of seedlings surviving until the 1st July after emergence on unburned and burned plots of the Dune-Area site planted in the 2nd, drier year. For each species and burn treatment, mean proportion surviving/2.5-m row and standard errors are presented.

episodic recruitment may be limited more by early survival of seedlings than by emergence itself. Similarly, Ackerman (1979) reported considerable natural emergence of shrubs at a Mojave–Great Basin transition site, but almost none of the seedlings survived beyond 2 yr. However, the absence of mature shrubs on our *Bromus*-dominated sites and the removal of some standing annual-plant litter during planting may have reduced seedling survival of shrubs in our experiment. Seedling survival of *Grayia* can be enhanced by litter and nurse plants (Shaw and Haferkamp 1994), and that of *Artemisia* by snow accumulation around shrubs (Sturges and Tabler 1981, Monsen et al. 1992).

A 2nd pattern of emergence was exhibited by the grasses *Agropyron* and *Pseudoroegneria* and the shrub *Ephedra*. In these species substantial emergence occurred over an extended period of time, from February into June. This pattern may be a bet-hedging adaptation (sensu Stearns 1976) similar to that of desert annuals for coping with the unpredictable climate of arid and semiarid regions (Went 1979, Freas and Kemp 1983, Philippi 1993). If rainy periods are cut short, annuals that germinate under ideal conditions may not be able to complete their life cycle. This risk is spread if, even under ideal conditions, some seeds remain dormant to germinate later. Similarly, the extended seasonal period of germination of these perennials may spread the risk of germinating in wet periods that are not long enough to allow seedlings sufficient growth to be able to survive summer drought. It may also afford these species greater potential to establish seedlings in any given year in an unpredictable environment because some seedlings can take advantage of wet periods whenever they occur from late winter to late spring. On the Near-Dune and Dune-Area sites, where conditions were less favorable or favorable less often, emergence of these "bet-hedging" species was more confined to the mid-spring period.

A 3rd pattern of emergence was displayed by the grasses *Elymus*, *Pascopyrum*, *Oryzopsis*, and *Stipa* and by the 2 forbs. Emergence began in April, later than that of species showing the first 2 patterns, and continued into June. Later emergence of *Elymus* than of *Pseudoroegneria* is consistent with laboratory results (Hardegree 1994).

The 4th pattern was that of the C_4 grasses *Pleuraphis* and *Sporobolus* for which all seedling emergence occurred after April. These species require warmer temperatures for emergence than any of the other species, and thus on Great Basin sites are usually dependent on late spring weather conditions.

As we used only a single accession of each species, our data do not represent the variation in emergence characteristics that can exist among different populations of some of these

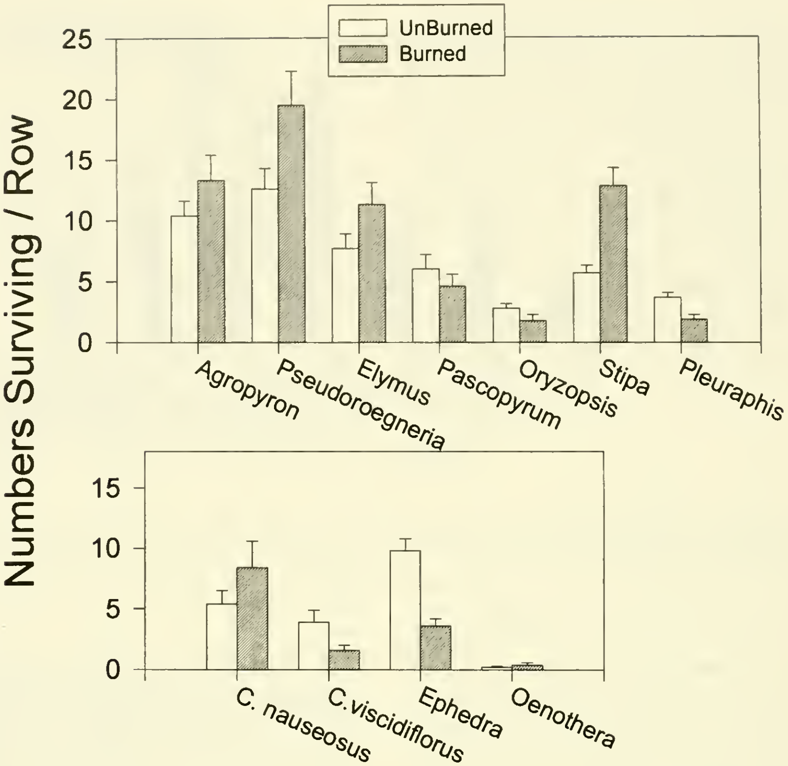

Fig. 7. Number of seedlings surviving until the 1st July after emergence on unburned and burned plots on the Hill site (species with nearly zero survival are omitted). For each species and burn treatment, mean number of seedlings surviving/3-m row and standard errors are presented.

species (e.g., Meyer and McArthur 1987, Meyer and Monsen 1992). However, the same pattern of emergence was often common to species within the same broad taxonomic or functional groups; e.g., the Asteraceae and Chenopodeaceae shrubs shared 1 pattern, the 2 forbs and 2 Stipeae another, and the C_4 grasses a 3rd pattern, suggesting that these general patterns are characteristic of some of these species or groups of species. Still, the 4 Triticeae displayed 2 different patterns. Some species, such as the 4 Triticeae, also can be expected to exhibit some autumn emergence, but none occurred in our study because planting was done too late for autumn emergence to occur.

Based on seasonal patterns of emergence observed in this experiment, different seasonal patterns of precipitation may favor either recruitment of shrubs or recruitment of grasses and forbs, largely to the exclusion of the other. Favorable winter and early spring moisture conditions could allow shrub establishment. In the drier year of the Dune-Area planting, early emergence of the *Chrysothamnus* species was almost nonexistent, and their emergence was lower overall relative to sites planted in the wetter year. A drier winter and early spring coupled with ample precipitation later might prevent shrub establishment but allow abundant recruitment of perennial grasses and forbs. Favorable moisture conditions even later could promote recruitment of *Pleuraphis*. Substantial *Pleuraphis* emergence and 1st-year survival occurred on both sites in the wetter year of 1994–95, but *Pleuraphis* failed to emerge on the Dune-Area site in the drier spring of 1996.

Site/Treatment Differences

Survival of *Agropyron* was lower on the Near-Dune than Hill site. *Agropyron* is considered unsuitable for sites with <20–25 cm annual precipitation (Young and McKenzie 1982). Precipitation at the nearest weather station exceeded this amount in the wet year of

1994–95 with 33 cm October–September. The Near-Dune site probably received at least this amount and the Hill site even more, but the Near-Dune site is more droughty because of its coarser soil. Our results are consistent with *Agropyron*'s unsuitablility for drier portions of the Great Basin. The native Triticeae, however, appeared better suited than *Agropyron* to these drier sites. In contrast to *Agropyron*, survival of *Elymus* did not differ between the Hill and Near-Dune sites. Comparable seedling emergence of *Pseudoroegneria* and *Agropyron* on the Hill site and similar to better survival of *Pseudoroegneria* are at odds with the commonly held concept of *Pseudoroegneria* having weak seedlings (e.g., Jones et al. 1991).

Stipa, Oryzopsis, Pleuraphis, and *Ephedra* appeared even better adapted to the drier Near-Dune site than did the native Triticeae. *Oryzopsis* is considered well adapted to sandy soils (Young et al. 1983), and this also appeared to be true of the other 3 species. In fact, their early survival tended to be higher on the Near-Dune than the Hill site, perhaps because *Bromus* was less abundant on the Near-Dune site. *Bromus* may have been less abundant because the Near-Dune site is a more stressful habitat for it. Notably, the site appeared more stressful for *Bromus* but not for seedlings of these 4 perennials.

On the Hill site February emergence of the chenopod shrubs was higher on burned than on unburned plots, while April emergence was often the reverse. This emphasizes how seedbed conditions can undergo rapid seasonal changes. In February the more open burned plots were apparently warmer but still moist, thus promoting emergence. In April the burned plots became drier, but the unburned plots were then warm enough to promote emergence and were still moist. The Triticeae showed a similar but less pronounced shift in response to burned and unburned plots from April to June.

A large effect of *Bromus* competition on seedlings was apparent. On the Dune-Area site, a drier site planted in a drier year, seedling survival of *Elymus, Pascopyrum*, and the 2 *Chrysothamnus* species was much better on burned than unburned plots. On this site, unlike the Hill site, burning greatly reduced *Bromus* abundance. Although the open burned plots were more exposed to drying, reduced competition from *Bromus* was apparently a much greater factor for seedling survival. *Chrysothamnus* survival was as high on these burned plots as on any treatment of our other 2 sites, suggesting *Chrysothamnus* seedlings are greatly affected by *Bromus* competition. In contrast, burned and unburned plots on the Hill site differed less in *Bromus* abundance, but unburned plots had more litter to reduce evaporation, and survival was generally similar on burned and unburned plots and, in fact, higher on unburned plots for *Pleuraphis* and *Ephedra*.

Species with Potential for Revegetation

Species with earlier seedling emergence are predicted to have better seedling survival in the face of competition from *Bromus*, which is thought to gain its competitive advantage through very early seedling emergence and growth (Young and Evans 1982, Hardegree 1994). Our early emerging *Chrysothamnus* and chenopod shrubs clearly did not support this, but the 2 early emerging grasses, *Pseudoroegneria* and *Agropyron*, showed good potential for establishment, at least on the Hill site, due to a combination of high emergence and high survival. Two later emerging grasses, *Elymus* and *Stipa*, also showed potential. *Ephedra*, another early emerging species, was the only shrub with good survival.

The Triticeae, especially *Agropyron*, showed less potential for establishment on drier sites, though *Pseudoroegneria* joined *Ephedra* and *Oryzopsis* as the only species with substantial seedling survival under the most severe conditions of our experiments, the unburned plots of the Dune-Area site with dry conditions and abundant *Bromus*. *Stipa* (not planted on the Dune-Area site) and *Ephedra* also had high numbers surviving on the other dry site, the Near-Dune site. *Oryzopsis* and *Pleuraphis* never had high numbers of seedlings surviving because they had low emergence. However, they may be useful for revegetation on drier sites because they consistently had high survival, even under severe conditions. *Pleuraphis* may largely escape competition from *Bromus* because its seedlings emerge in late spring when *Bromus* has completed most of its growth.

Consequences of Different Seasonal Patterns of Emergence

There were some distinct differences in seedling emergence between the 2 yr of our experiment. In 1995, with more precipitation in both winter and spring, there was considerable February emergence of *Chrysothamnus* and considerable emergence of *Pleuraphis* in late spring, while in 1996 such very early emergence of *Chrysothamnus* was almost nonexistent, and there was no emergence of *Pleuraphis*. A wider sampling of years might reveal considerable temporal segregation of recruitment of different species into different years due to different years having seasonal patterns of precipitation favorable to recruitment of different species. As most of these species are long lived, and yearly variation in precipitation is likely to affect survival of established plants less severely than it affects recruitment, much of the gain in abundance that each species makes in years favorable to its recruitment is likely to remain through unfavorable periods. This temporal separation of recruitment of different species with a considerable lag in the removal of individuals recruited can lead to a greater number of species on the site than would exist without variation among years (storage effect; Chesson 1994).

Although variation in the pattern of precipitation at the scale of years can promote greater species coexistence, Neilson (1986) linked major and persistent shifts in vegetation composition in the Chihuahuan Desert region to species-specific or species group–specific responses to decades-long changes in seasonal patterns of precipitation. Intensification of monsoonal summer precipitation in the western USA is a major prediction of many global climatic change scenarios (Lin et al. 1996). Changes in precipitation patterns of the Great Basin to more summer precipitation, with more frequent El Niño events and/or global warming, could cause shifts to greater recruitment of grasses, particularly C_4 grasses, and reduced recruitment of shrubs.

Knowledge of seasonal patterns of seedling emergence of different species could be useful in rangeland vegetation management if used in an opportunistic rangeland management approach (sensu Westoby et al. 1989). Establishment of shrubs, C_3 grasses and forbs, and C_4 grasses could be considered as 3 possible alternative states, along with a catalog of conditions (i.e., seasonal patterns of precipitation) that should induce a transition to each of these states. A desired transition could be attempted when the necessary conditions appear likely (e.g., seed C_3 grasses when a wet spring is predicted). It should also be noted that years with reduced precipitation in winter and early spring, periods important to *Bromus*, could provide an enhanced opportunity for recruitment of other species on *Bromus*-dominated sites.

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BUTTERFLIES OF THE TOQUIMA RANGE, NEVADA: DISTRIBUTION, NATURAL HISTORY, AND COMPARISON TO THE TOIYABE RANGE

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ABSTRACT.—Studies of Great Basin faunas can provide information for landscape-level adaptive management by federal agencies and shed light on potential effects of climate change in continental interior landscapes. To provide such information, we characterized the butterfly fauna of the Toquima Range, a mountain range in the heart of the Great Basin with topography typical of the region. We also compared the butterfly fauna of the Toquima Range to that of the adjacent Toiyabe Range, which is more topographically complex and species rich but less representative of the Great Basin on the whole. We explicitly addressed the effects of area and water availability on butterfly species richness. Butterfly species presence data were compiled for 14 canyons and 1 peak in the Toquima Range. Data from 11 canyons that we inventoried systematically were amenable to statistical analysis. Eighty butterfly species (59 residents) have been recorded from the Toquima Range since 1935. By comparison, 99 species have been recorded from the Toiyabe Range. Mean canyon-level butterfly species richness was significantly lower in the Toquima Range than in the Toiyabe Range. This difference cannot be explained by differences in canyon size between the mountain ranges. Within the Toquima Range water availability seems to have a dominant effect on butterfly species richness. Between mountain ranges species richness is influenced by interactions among area, moisture, and topography. These data should assist managers in developing guidelines for conservation planning in the Great Basin.

Key words: Toquima Range, Toiyabe Range, butterflies, species richness, riparian habitat, conservation, ecosystem management.

One of Earth's forlorn landscapes, the high desert is bitterly cold in winter, stifling hot in summer, and dry. Situated in an effective rain shadow, the Great Basin encompasses nearly 430,000 km^2 of internal drainage extending from the east slope of the Sierra Nevada and southern Cascades to the west, the west slope of the Wasatch Range to the east, the Columbia River to the north, and the Colorado River to the south (Grayson 1993). At the austere center of the Great Basin lies the Toquima Range. At first glance the Toquima Range is unremarkable. It is neither particularly extensive in area nor, for most of its crest, especially high in elevation. Riparian canyons, known in arid regions for their concentrations of plants and wildlife (Kauffman and Krueger 1984, Armour et al. 1991, Dawson 1992, Dobkin et al. 1998), are the exception rather than the rule in the Toquima. Prominent topographic features, including lakes and pronounced peaks that attract tourists and backcountry enthusiasts, are largely absent from the range. Yet the geography, biology, anthropological history, and even politics of the Toquima Range encapsulate the Great Basin. We were drawn to study the butterfly fauna of the Toquima Range not only because the range is the literal and figurative heartland of the Great Basin, but also to compare it with that of the Toiyabe Range, a neighboring range with subalpine peaks and incised canyons that are far more spectacular, but considerably less typical of the Great Basin as a whole (Trimble 1989, Grayson 1993, Fleishman et al. 1997).

Few studies of Great Basin butterflies have concentrated on the region's center. Compared to faunas present in the Sierra Nevada and Rocky Mountains, central Great Basin butterflies as a group are neither notably rich in species nor in endemic taxa (Wilcox et al. 1986, Austin and Murphy 1987) and have attracted relatively few amateur and professional biologists. However, the region provides an excellent template for research on the potential effects of climate change on butterfly and other animal and plant communities in temperate continental interior landscapes (e.g., McDonald and Brown 1992, Murphy and Weiss 1992, Fleishman et al. 1998). Moreover, federal and state agencies responsible for maintaining viable populations of animals and plants in the Great Basin are eager for data on community composition and broad-scale ecological patterns; these data are needed to implement effective landscape-level and adaptive management in the region (Stohlgren et al. 1995, Czech and Krausman 1997, Lambeck 1997, Heikkinen 1998, Simberloff 1998).

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The definitive faunal study of central Great Basin butterflies to date (Fleishman et al. 1997) was conducted in the Toiyabe Range, a scant 10 km to the west of the Toquima Range. Also centrally located, the Toiyabe Range is unusually large (3126 km^2; see Biological Resources Research Center [BRRC] 1997), mesic, and biologically diverse relative to many Great Basin ranges (Trimble 1989, Grayson 1993). With a crest that exceeds 3000 m for 40% of its length, it accumulates a substantial snowpack that replenishes streams and delays senescence of riparian and upland vegetation. Biological patterns in a more "typical" Great Basin mountain range, such as the Toquima, arguably may have greater generality. In addition, because the Toquima and Toiyabe ranges have similar biogeographic and management histories (Murphy and Wilcox 1986, Wilcox et al. 1986, Austin and Murphy 1987), our research allowed us to address the effects of area and water availability on butterfly species richness in arid regions.

STUDY AREA

The Toquima Range is located in Lander and Nye counties, Nevada, less than 10 km from the geographic center of the state (Grayson 1993, BRRC 1997; Fig. 1). The 125-km-long, 1750-km^2 range is roughly linear and, typical of most Great Basin mountains, oriented north–south. Roughly 90% of its crest lies at about 2700 m, approximately 500–600 m above Big Smoky Valley to the west and Monitor Valley to the east. A 13-km stretch of the Mount Jefferson ridgeline, with 3 summits above 3300 m, rises above the rest of the Toquima crest (Grayson 1993). Compared to much of the Toquima Range, the local climate of Mount Jefferson is atypically cold (up to 10°C cooler near the top than at the base of the peak on a clear day) and mesic (Trimble 1989, Hidy and Klieforth 1990, E. Fleishman personal observation). Numerous canyons cut the east and west slopes of the Toquima Range. A few of these canyons have perpetually flowing streams, and several have seeps or springs, but most are dry. Topography of individual canyons varies widely.

With increasing elevation in the Toquima Range, dominant vegetation shifts from sagebrush (*Artemisia tridentata* ssp.) to piñon-juniper (*Pinus monophylla*, *Juniperus osteosperma*) woodland to low brush (Tueller and Eckert 1987). A limber pine (*Pinus flexilis*) krummholz grows at timberline, and the summit slopes of Mount Jefferson are inhabited by a depauperate alpine flora (Trimble 1989, Grayson 1993). Patches of mountain mahogany (*Cercocarpus ledifolius*) occur within and above the piñon-juniper zone, and aspen (*Populus tremuloides*) grows in riparian canyons and around seeps on exposed slopes. Canyons with permanent or ephemeral surface water often have willow (*Salix* spp.), rose (*Rosa woodsii*), nettle (*Urtica dioica*), and an understory composed of various grasses and forbs. Two plants considered sensitive by federal agencies, Toquima milkvetch (*Astragalus toquimanus*) and Toiyabe buckwheat (*Eriogonum esmaraldensis toiyabensis*), occur in the mountain range (J. Brack personal communication).

More than 99% of the Toquima Range is federally owned. The U.S. Forest Service oversees 88% of the range, and the Bureau of Land Management controls 11% (BRRC 1997). Thus, the majority of income-generating activities in the Toquima Range, including livestock grazing and mining, must be approved by the appropriate federal agency. This has caused considerable conflict between agencies and some local residents, who contend that the rightful owners of public lands are the counties rather than the federal goverment (Egan 1995, Larson 1995, USFS 1995). Two of the most publicized battles in the recent history of the "Sagebrush Rebellion" have been fought in the Toquima Range—the unauthorized opening (by bulldozer) of a Forest Service road in Jefferson Canyon by Nye County Commissioner Dick Carver, and the Forest Service's impoundment of cattle owned by rancher Wayne Hage in Pine Creek Canyon.

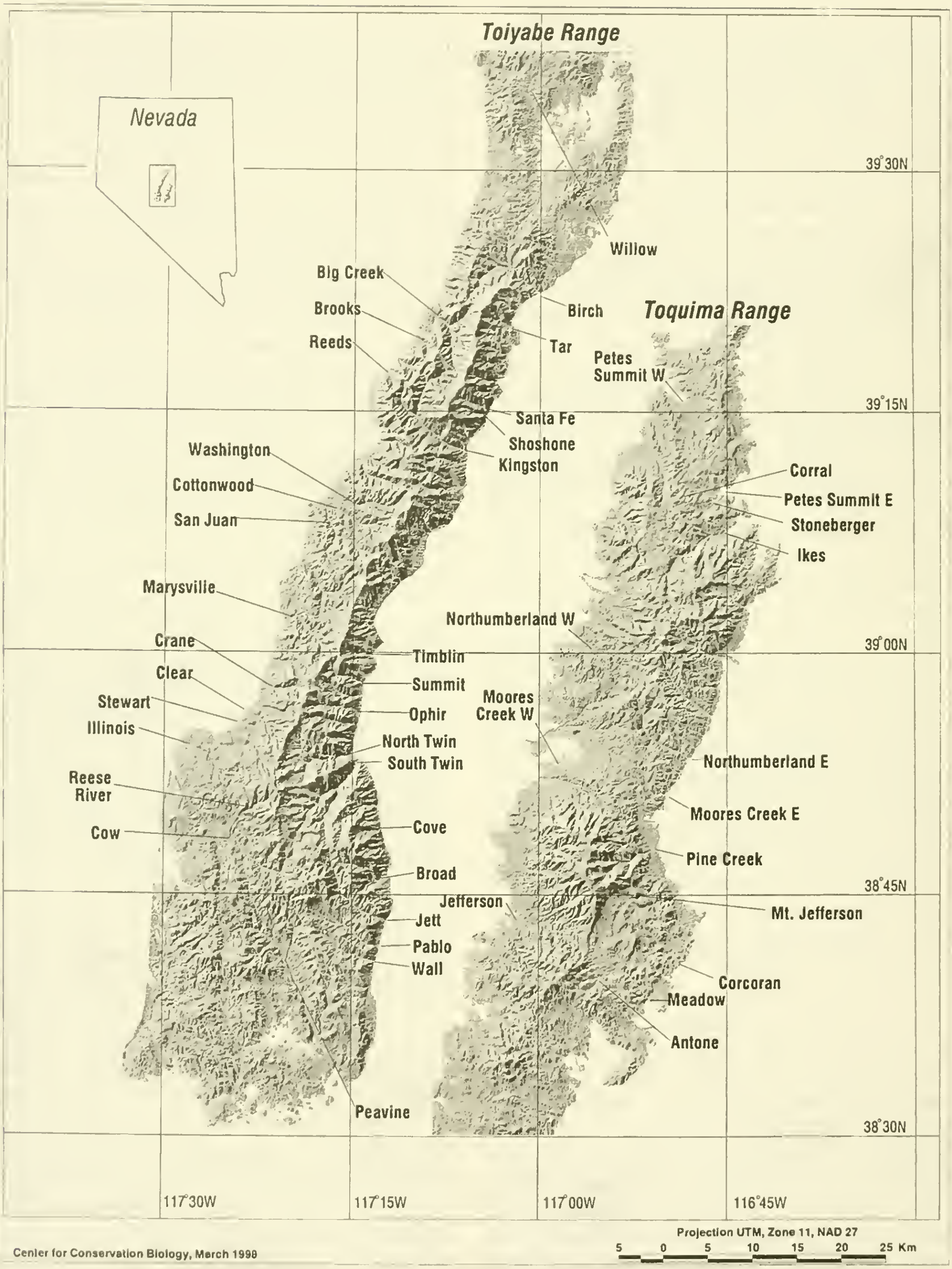
Toiyabe Range
Nevada
39°30N
Willow
Big Creek
Brooks
Reeds
Birch
Tar
Toquima Range
Petes Summit W
39°15N
Santa Fe
Shoshone
Kingston
Washington
Cottonwood
San Juan
Corral
Petes Summit E
Stoneberger
Ikes
Marysville
Northumberland W
39°00N
Crane
Clear
Stewart
Illinois
Timblin
Summit
Ophir
Moores Creek W
North Twin
South Twin
Northumberland E
Reese River
Cow
Cove
Moores Creek E
Pine Creek
Broad
38°45N
Jefferson
Mt. Jefferson
Jett
Pablo
Wall
Corcoran
Meadow
Antone
Peavine
38°30N
117°30W
117°15W
117°00W
116°45W
Projection UTM, Zone 11, NAD 27
5 0 5 10 15 20 25 Km
Center for Conservation Biology, March 1998

Fig. 1. Study canyons in the Toquima and Toiyabe ranges and their position within Nevada (inset).

METHODS

We compiled species presence data for 14 canyons in the Toquima Range and for Mount Jefferson from specimens in private and institutional collections, field notes of experienced lepidopterists, a systematic inventory conducted in the mid-1980s, and a systematic inventory conducted in 1996 and 1997. One canyon was included in the 1980s inventory, and 10 canyons were included in the 1990s inventory (Fig. 1). Five canyons were inventoried in both 1996 and 1997, 4 in 1996 only, and 1 in 1997 only. To account for differences in flight phenology among species and locations, we inventoried each canyon roughly every 2 wk throughout the majority of the flight season (May–August). During canyon visits we walked the length of each canyon at a constant pace and recorded presence of all butterfly species seen. Walking transects are a standard technique for surveying butterfly communities (Shapiro 1975, Pollard 1977, Thomas and Mallorie 1985, Swengel 1990, Kremen 1992, Pollard and Yates 1993, Harding et al. 1995). When necessary, individual butterflies were caught and either identified on site or held for later identification. Voucher specimens were deposited at the University of Nevada, Reno and at the Nevada State Museum and Historical Society, Las Vegas. Our nomenclature largely follows that of Austin (in press).

We did not attempt to quantify abundances of all butterfly species recorded from the Toquima Range because, particularly over a relatively short (2-yr) time period, estimation of abundance is complicated by factors including interspecific variation in population structure, sensitivity to short-term climatic fluctuations, and staggered emergence (Shapiro 1975, Scott 1986). However, we did categorize each butterfly species with respect to its qualitative relative abundance in its principal habitat at the peak of its flight season in the Toquima Range (Fleishman et al. 1997). We established 6 relative abundance categories: abundant (generally seen and in large numbers), common (generally seen but not in large numbers), fairly common (generally seen but in small numbers or not generally seen), uncommon (seldom seen but not a surprise), rare (presence always a surprise but not far out of normal range), and accidental (far out of normal range).

Toquima Range canyons are frequently narrow and steeply walled. Canyon bottoms are the most accessible areas in the Toquima Range, and virtually all resident butterflies in the Toquima Range occur there (Fleishman et al. 1997). Therefore, we defined the area that our transects sampled ("canyon area") as 50 m on either side of the inventory route. To calculate this area, we recorded the location of our 1990s inventory transects with differentially corrected Global Positioning Systems (GPS), which are accurate within 5 m. GPS positions were then overlaid on a 30-m Digital Elevation Model of the central Great Basin maintained on a Geographic Information System (GIS).

We used analysis of variance to test whether there was a significant difference in mean number of species and canyon area among Toquima Range and Toiyabe Range canyons that were inventoried systematically over the past 4 yr (1994–1997). Eleven Toquima Range canyons and 19 Toiyabe Range canyons were included in these tests (see Fig. 1). The same methods were used to inventory Toiyabe Range and Toquima Range canyons. A detailed description of Toiyabe Range natural history, study locations, and inventory results is presented in Fleishman et al. (1997).

RESULTS

Eighty butterfly species have been recorded from the Toquima Range since 1935 (Table 1). Species richness of individual canyons ranged from a high of 66 species in Meadow Canyon to a low of 26 in Corral Canyon. Twenty-seven species have been recorded from Mount Jefferson. Species richness of the 11 canyons we inventoried systematically ranged from 66 (Meadow Canyon) to 33 (Petes Summit West), with a mean of 50. Of the latter group of canyons, 5 have flowing streams, 5 have localized seeps or springs, and 1 is dry (Table 1).

Fifty-nine butterfly species recorded from the Toquima Range most likely are resident, i.e., complete their entire life cycle in the Toquima Range (Table 2). Of these species, 25 are restricted to montane habitats and do not occur in valleys in the vicinity of the Toquima Range (Table 2). Two species that occur regularly in the Toquima Range, *Vanessa cardui* and *Danaus plexippus*, are true migrants (Scott 1986). Some individuals of 1 resident species (*Nymphalis antiopa*) may migrate. An additional 18 species are frequent or infrequent

TABLE 1. Canyon-level butterfly distribution records, Toquima Range, Lander and Nye counties, Nevada. Water codes: 1 = flowing stream, 2 = seep or spring. Location codes: PW = Petes Summit, west side; NW = Northumberland, west side; MW = Moores Creek, west side; JF = Jefferson; PT = Petes Summit, east side; CA = Corral; SB = Stoneberger; IK = Ikes; NE = Northumberland, east side; ME = Moores Creek, east side; PI = Pine Creek; CN = Corcoran; AN = Antone; MD = Meadow; MJ = Mount Jefferson.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Resident															
HESPERIIDAE															
Erynnis icelus (Scudder & Burgess)															x
Erynnis persius (Scudder)	x	x		x	x	x	x	x	x		x		x	x	x
Hesperia uncas W.H. Edwards ssp.	x	x	x	x	x	x	x	x		x				x	x
Hesperia juba (Scudder)	x	x	x	x	x	x	x	x	x	x		x	x	x	
Hesperia comma harpalus (W.H. Edwards)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Ochlodes sylvanoides bonnevilla Scott		x	x	x			x		x	x		x	x	x	
PAPILIONIDAE															
Papilio zelicaon Lucas				x										x	x
Papilio indra nevadensis T. & J. Emmel				x							x				
Papilio rutulus rutulus Lucas		x	x	x	x	x	x	x		x	x	x	x	x	x
Papilio multicaudatus W.F. Kirby ssp.				x			x				x	x	x	x	
PIERIDAE															
Neophasia menapia (C. & R. Felder) ssp.	x	x	x	x	x		x		x			x		x	
Pontia beckerii beckerii (W.H. Edwards)	x	x	x	x	x		x	x	x	x		x	x	x	
Pontia sisymbrii elivata (Barnes & Benjamin)		x					x							x	
Euchloe ausonides (Lucas) ssp.		x	x	x	x			x							
Euchloe hyantis lotta Beutenmüller			x				x						x		
Anthocharis sara thoosa (Scudder)			x		x	x	x						x	x	
Colias philodice eriphyle W.H. Edwards							x							x	
Colias alexandra edwardsii W.H. Edwards	x	x	x	x	x		x	x	x	x	x	x	x	x	x
LYCAENIDAE															
Lycaena arota virginiensis (W.H. Edwards)				x					x	x		x		x	
Lycaena rubidus sirius (W.H. Edwards)							x	x				x	x	x	
Lycaena heteronea Boisduval ssp.		x	x	x				x	x	x	x		x	x	
Lycaena helloides helloides (Boisduval)				x	x	x	x						x		
Harkenclenus titus immaculosus (W.P. Comstock)														x	
Satyrium behrii crossi (Field)	x	x	x	x	x		x		x	x		x	x	x	

TABLE 1. Continued.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Satyrium californicum (W.H. Edwards) ssp.				x	x			x		x			x	x	
Satyrium sylvinum putnami (Hy. Edwards)			x	x	x		x					x	x	x	
Callophrys affinis affinis (W.H. Edwards)		x	x	x	x				x	x	x		x	x	x
Loranthomitoura spinetorum spinetorum (Hewitson)	x	x			x						x				
Mitoura siva chalcosiva (Clench)	x	x	x	x	x		x		x	x				x	
Incisalia eryphon (Boisduval) ssp.	x	x	x	x	x		x		x	x	x	x	x	x	
Everes amyntula herrii F. Grinnell		x		x	x		x		x	x	x			x	
Celastrina ladon echo (W.H. Edwards)							x			x	x			x	
Euphilotes enoptes (Boisduval) ssp.	x	x		x	x	x	x		x	x	x		x	x	x
Glaucopsyche piasus nevada F.M. Brown				x		x	x		x	x	x	x	x	x	x
Glaucopsyche lygdamus oro (Scudder)		x		x						x					
Lycaeides melissa paradoxa (F.H. Chermock)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Plebejus saepiolus (Boisduval) ssp.		x	x	x		x	x	x		x	x	x	x	x	x
Icaricia icarioides fulla (W.H. Edwards)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Icaricia shasta (W.H. Edwards) ssp.		x	x	x			x	x	x	x	x		x	x	x
Icaricia acmon texana (Goodpasture)					x	x	x	x	x	x	x			x	x
Icaricia lupini (Boisduval) ssp.	x	x	x	x	x	x	x		x	x	x	x	x	x	x
Apodemia mormo mormo (C. & R. Felder)	x	x	x	x	x		x		x	x		x		x	
NYMPHALIDAE															
Speyeria coronis snyderi (Skinner)		x			x										
Speyeria zerene gunderi (J.A. Comstock)		x	x				x		x			x	x	x	
Speyeria callippe harmonia dos Passos & Grey	x	x		x	x	x	x	x	x				x	x	x
Thessalia leanira alma (Strecker)	x				x										
Chlosyne acastus acastus (W.H. Edwards)		x	x	x		x	x	x	x	x	x	x	x	x	
Phyciodes pulchella (Boisduval) ssp.		x	x	x		x	x	x			x		x	x	
Phyciodes mylitta mylitta (W.H. Edwards)				x			x		x		x	x	x	x	
Euphydryas anicia wheeleri (Hy. Edwards)	x	x	x	x	x	x	x	x	x	x		x	x	x	
Euphydryas editha lehmani Gunder	x	x	x	x	x	x	x	x	x	x			x	x	x

TABLE 1. Continued.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Polygonia zephyrus (W.H. Edwards)		x	x	x			x				x	x	x	x	x
Nymphalis antiopa antiopa (Linnaeus)	x	x	x	x	x	x	x	x			x	x	x	x	
Nymphalis milberti subpallida (Cockerell)		x				x	x			x	x			x	x
Limenitis weidemeyerii latifascia E.M. & S.F. Perkins	x	x	x	x	x		x	x	x	x	x	x	x	x	
Coenonympha tullia (Müller) spp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Cercyonis sthenele paulus (W.H. Edwards)	x	x	x	x	x		x		x	x	x	x	x	x	
Cercyonis oetus oetus (Boisduval)	x	x	x	x		x	x	x	x	x	x	x	x	x	x
Neominois ridingsii stretchii (W.H. Edwards)	x	x	x	x	x		x	x	x	x				x	
SUBTOTAL	26	41	35	45	35	23	46	26	33	35	30	29	38	50	22
Migrant or Immigrant															
HESPERIIDAE															
Pyrgus scriptura (Boisduval) ssp.		x		x											
Pyrgus communis communis (Grote)	x	x	x	x	x		x		x	x		x	x	x	
Heliopetes ericetorum (Boisduval)		x											x	x	
PIERIDAE															
Pontia protodice (Boisduval & Le Conte)	x	x	x	x	x		x		x	x	x	x	x	x	
Pontia occidentalis occidentalis (Reakirt)	x	x						x						x	x
Pieris rapae rapae (Linnaeus)														x	
Colias eurytheme Boisduval	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Nathalis iole Boisduval							x								
LYCAENIDAE															
Strymon melinus pudica (Hy. Edwards)		x	x	x									x	x	
Leptotes marina (Reakirt)			x							x	x			x	x
Brephidium exilis exilis (Boisduval)		x	x	x	x					x	x	x	x	x	
Hemiargus isola alce (W.H. Edwards)										x					
NYMPHALIDAE															
Vanessa virginiensis (Drury)							x							x	
Vanessa cardui (Linnaeus)	x	x	x		x	x	x			x	x		x	x	x
Vanessa annabella (Field)		x				x	x	x						x	x
Vanessa atalanta rubria (Fruhstorfer)							x				x			x	
Junonia coenia Hübner	x														

TABLE 1. Continued.

	Canyons (north to south)														
	West slope				East slope										
	PW	NW	MW	JF	PT	CA	SB	IK	NE	ME	PI	CN	AN	MD	MJ
Systematic inventory	x	x	x	x	x		x		x	x		x	x	x	
Water	2	2	2	1	2	1	1	2		2	1	1	1	1	
Danaus plexippus plexippus (Linnaeus)		x		x			x	x		x		x	x	x	
SUBTOTAL	6	11	7	7	5	3	9	4	3	8	6	5	8	14	5
Marginal or Accidental															
HESPERIIDAE															
Hesperopsis libya lena (W.H. Edwards)	x	x	x												
PAPILIONIDAE															
Battus philenor philenor (Linnaeus)														x	
PIERIDAE															
Eurema mexicana mexicana (Boisduval)							x							x	
SUBTOTAL	1	1	1				1							2	
TOTAL	33	53	43	52	40	26	56	30	36	43	36	34	46	66	27

immigrants to the Toquima Range (whether or not the species breed in the Toquima, they probably cannot survive all winters in the range; Table 2). *Hesperopsis libya* sometimes strays into the Toquima Range from Big Smoky Valley to the west; there may be some localized populations of the species on the west slope of the Toquima Range. Single *Battus philenor* and *Eurema mexicana*, well outside their usual distributional range (Scott 1986), have been recorded from the Toquima Range.

Fourteen species recorded from the Toquima Range, including 13 residents, are riparian obligates (Table 2). We define riparian obligate species as those that could not maintain permanent populations in the absence of a riparian zone because their larval host plants do not or rarely occur away from dependable water (Fleishman et al. 1997).

Of 59 resident butterfly species in the Toquima Range, 8 are abundant. Ten resident and 1 immigrant species are common. A total of 28 species, 23 resident and 5 migrant or immigrant, are fairly common. Eleven resident, 5 migrant or immigrant, and 1 marginal species are uncommon, while 14 species (7 resident and 7 immigrant) are rare.

All resident butterfly species and all but 3 nonresident species (*Pyrgus scriptura*, *B. philenor*, and *E. mexicana*) recorded from the Toquima Range also have been recorded from the Toiyabe Range. In a previous paper (Fleishman et al. 1997), we presented data on the life history of Toiyabe Range butterflies. Most data that are applicable across the 2 mountain ranges are not repeated here. These data included each species' geographic distribution (relative position of the Toquima Range within its geographic range and its subspecific-level biogeographic affinity), potential host plants in the Toquima Range, relative annual fluctuation in abundance, habitat in which the butterfly most frequently is observed (including riparian canyons, all canyons, and uplands), and habitat use (patrolling habitat, perching habitat, and relative use of mud puddles).

The mean number of species recorded from Toquima Range canyons was significantly less than the mean number of species recorded from systematically inventoried Toiyabe Range canyons. This result was consistent for resident species (Toquima mean = 37, Toiyabe mean = 48, $F_{.05[1,27]} = 11.029$, $P < 0.005$), nonresident species (Toquima mean = 8, Toiyabe mean = 13, $F_{.05[1,27]} = 9.832$, $P < 0.005$), and all species (Toquima mean = 45, Toiyabe mean = 61, $F_{.05[1,27]} = 11.622$, $P < 0.005$). Although species richness tends to increase with canyon area in

TABLE 2. Life history traits of butterflies recorded from the Toquima Range. Montane species are restricted to montane habitats; individuals of these species rarely if ever occur in valleys in the Toquima Range vicinity. Riparian obligate species are those that could not maintain permanent populations in the absence of a riparian zone because their larval host plants do not or rarely occur away from dependable water. Relative abundance categories are abundant (generally seen and in large numbers), common (generally seen but not in large numbers), fairly common (generally seen but in small numbers or not generally seen), uncommon (seldom seen but not a surprise), rare (presence always a surprise but not far out of normal range), and accidental (far out of normal range).

Species	Montane	Riparian obligate	Relative abundance
RESIDENT			
Erynnis icelus	x	x	rare
Erynnis persius	x		uncommon
Hesperia uncas	x		fairly common
Hesperia juba			abundant
Hesperia comma			abundant
Ochlodes sylvanoides			fairly common
Papilio zelicaon	x		rare
Papilio indra	x		rare
Papilio rutulus	x	x	fairly common
Papilio multicaudatus	x	x	fairly common
Neophasia menapia	x		common
Pontia beckerii			common
Pontia sisymbrii	x		uncommon
Euchloe ausonides	x		fairly common
Euchloe hyantis			uncommon
Anthocharis sara	x		fairly common
Colias philodice		x	uncommon
Colias alexandra			common
Lycaena arota	x		fairly common
Lycaena rubidus		x	fairly common
Lycaena heteronea	x		common
Lycaena helloides		x	uncommon
Harkenclenus titus	x	x	rare
Satyrium behrii	x		fairly common
Satyrium californicum	x		fairly common
Satyrium sylvinum		x	fairly common
Callophrys affinis	x		uncommon
Loranthomitoura spinetorum	x		rare
Mitoura siva	x		fairly common
Incisalia eryphon	x		common
Everes amyntula			fairly common
Celastrina ladon	x		uncommon
Euphilotes enoptes	x		fairly common
Glaucopsyche piasus	x		fairly common
Glaucopsyche lygdamus			fairly common
Lycaeides melissa			common
Plebejus saepiolus		x	uncommon
Icaricia icarioides	x		abundant
Icaricia shasta	x		common
Icaricia acmon			uncommon
Icaricia lupini	x		fairly common
Apodemia mormo			common
Speyeria coronis	x		rare
Speyeria zerene	x		fairly common
Speyeria callippe	x		uncommon
Thessalia leanira	x		rare
Chlosyne acastus	x		abundant
Phyciodes pulchella	x		fairly common
Phyciodes mylitta			fairly common
Euphydryas anicia	x		abundant
Euphydryas editha	x		fairly common
Polygonia zephyrus	x		fairly common
Nymphalis antiopa	x		fairly common
Nymphalis milberti	x		uncommon

TABLE 2. Continued.

Species	Montane	Riparian obligate	Relative abundance
Limenitis weidemeyerii			common
Coenonympha tullia			abundant
Cercyonis sthenele	x		abundant
Cercyonis oetus			abundant
Neominois ridingsii	x		common
MIGRANT OR IMMIGRANT			
Pyrgus scriptura			rare
Pyrgus communis			fairly common
Heliopetes ericetorum			common
Pontia protodice			fairly common
Pontia occidentalis			uncommon
Pieris rapae	x		uncommon
Colias eurytheme			fairly common
Nathalis iole			rare
Strymon melinus			rare
Leptotes marina			rare
Brephidium exilis			fairly common
Hemiargus isola			rare
Vanessa virginiensis			rare
Vanessa cardui			uncommon
Vanessa annabella			uncommon
Vanessa atalanta	x		rare
Junonia coenia			uncommon
Danaus plexippus			fairly common
MARGINAL OR ACCIDENTAL			
Hesperopsis libya			uncommon
Battus philenor			accidental
Eurema mexicana			accidental

both ranges (Fleishman et al. unpublished manuscripts), the mean area of Toquima and Toiyabe Range canyons was not significantly different (Toquima mean = 99.2 ha, Toiyabe mean = 85.7 ha, $F_{.05[1,21]} = 1.222$, $P = 0.28$). In other words, the difference in species richness between Toquima and Toiyabe Range canyons cannot be explained by differences in canyon size between the 2 ranges.

DISCUSSION

Knowledge of species distributions and coarse-grained species richness patterns is critical to conservation planning exercises including reserve design, land-use decision making, and adaptive management (Doak and Mills 1994, Stohlgren et al. 1995, Lambeck 1997, Longino and Colwell 1997, Mac Nally 1997, Simberloff 1998). Documenting butterfly distributions not only has intrinsic merit, but also could prove valuable because butterflies widely are thought to be sensitive to anthropogenic disturbances and able to provide an early warning of ecological change (Noss 1990, Kremen et al. 1993, New et al. 1995, Hamer et al. 1997).

Within the Toquima Range, moisture appears to be a primary factor affecting butterfly species richness at the canyon level. Water may enhance plant species richness and help both to prolong the temporal window for plant growth and flowering and to maintain muddy patches used by adult butterflies (Murphy and Wilcox 1986). Of the 11 canyons we inventoried systematically, the 2 with the greatest number of resident butterfly species have running streams, and the 8 richest canyons all have either running streams or seeps. Canyons rich in butterflies also tend to be topographically heterogeneous; thus, they tend to have diverse microclimatic zones and plant communities as well as sites for perching and patrolling by butterflies.

Several interacting factors, including area, moisture, and topography, probably contribute to species richness at the level of mountain ranges. The effects of area on species richness may be more significant at the level of mountain ranges than at the level of canyons. Thus, the larger area of the Toiyabe Range relative to the Toquima Range as a whole (as opposed to the area of their constituent canyons) may help explain why more butterfly species occupy the Toiyabe than the Toquima Range. Often, as is the case with the Toiyabe and Toquima ranges, larger ranges have greater topographic and vegetational diversity than smaller ranges (Grayson 1993). In addition, larger ranges might have, on average, more populations per species than smaller ranges, which decreases the risk of stochastic species extirpations within mountain ranges (Gilpin and Soulé 1986, Rabinowitz et al. 1986).

The difference in moisture availability between the Toquima and Toiyabe ranges, which is driven partly by their topographic differences, also may help explain why the Toquima Range has fewer butterfly species than the Toiyabe Range. In the Great Basin, ranges like the Toquima that are moderately small and low tend to be more arid than relatively large and tall ranges (e.g., the Toiyabe Range). Annual precipitation estimates obtained from the orographic precipitation model PRISM (Parameter-elevation Regressions on Independent Slopes Model; Daly et al. 1994) indicate that annual precipitation in a given canyon in the Toquima Range is not substantially less than precipitation in a given canyon in the Toiyabe Range. However, crests of larger and higher ranges capture more winter snow (which accounts for most of the effective precipitation in the Great Basin; Trimble 1989, Hidy and Klieforth 1990, Grayson 1993) and retain their snowpack later in the year than do smaller ranges. Gradual snowpack melting appears to replenish streams and may delay vegetation senescence, including larval host plants and adult nectar sources.

Eleven resident butterfly species recorded from the Toiyabe Range have not been recorded from the Toquima Range. There are parsimonious explanations for most of these apparent absences. Distributions of 4 species recorded from the Toiyabe but not the Toquima, *Pholisora catullus*, *Lycaena nivalis*, *Incisalia augustinus*, and *Speyeria egleis*, are either relictual or indicative of more recent dispersal from elsewhere, probably the northeastern Great Basin (Fleishman et al. 1997). The Toiyabe Range is the only central Great Basin location in which these 4 species have been recorded. Similarly, the only central Great Basin record of *Lycaena editha* is from the Toiyabe. An isolated population of *Ochlodes yuma* is associatied with a small patch of its host plant, *Phragmites australis*, on the east slope of the Toiyabe Range (Fleishman et al. 1997). Although there are several records of *Callophrys comstocki* and *Polygonia satyrus* from the Toiyabe Range, we did not encounter either species in that range during butterfly inventories in the 1990s. Likewise, only 1 *Euphilotes battoides* was recorded from the Toiyabe Range in the 1990s. Finally, the apparent absence of *C. comstocki*, *E. battoides*, and *Incisalia fotis* may reflect sampling error. These 3 species fly extremely early in the season and are rare.

Two species remain whose apparent absence from the Toquima Range is surprising—*Papilio bairdii* and *Speyeria nokomis*. Host plants and habitat that seem suitable for both species occur in the Toquima Range. However, both species principally are found in riparian canyons; streams and seeps in the Toquima Range often are isolated. Suitable habitat patches in the Toquima Range may be too distant from each other and from occupied habitats outside the range for immigration to occur regularly and for the species to maintain viable populations in the Toquima Range (Murphy et al. 1990, Hanski 1991, Hanski and Gilpin 1991).

Examination of species richness and composition within and among mountain ranges can have a significant bearing on management of rugged, remote landscapes like the Great Basin. Knowledge of "what is where" and why some areas have more species than others (particularly if species richness responds to factors that can be influenced by management) is critical to scientifically informed conservation planning. Not only do distributional data assist managers in delineating land uses, but they also can help managers and researchers predict and evaluate effects of experimental management strategies such as prescribed burning or alternative grazing schemes. The ecology of the Toquima Range may elicit few superlatives, but this very fact makes the range an excellent model for examining Great Basin species distributions across spatial scales critical to conservation planning.

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CLASSIFICATION AND ORDINATION OF THE ALPINE PLANT COMMUNITIES OF RAILROAD RIDGE, WHITE CLOUD PEAKS, IDAHO

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ABSTRACT.—Alpine vegetation of Railroad Ridge in the White Cloud Peaks, Custer County, Idaho, was investigated to ascertain native communities and describe their distribution with respect to important environmental factors. Percent cover of all species and environmental information were recorded for 69 plots. Data were analyzed by TWINSPAN and CANOCO, which provided a classification and an ordination, respectively. Predominant communities are dominated by (1) *Phlox pulvinata*, (2) *Carex elynoides*, and (3) *Geum rossii*, and other communities of lesser importance are dominated by (4) *Artemisia campestris*, (5) *Eriogonum ovalifolium* and *Silene acaulis*, and (6) *Ivesia gordonii*. Although the *Artemisia campestris* community occupies a relatively small portion of the study area, it is noteworthy because it is a community type not previously known for Idaho. The community co-dominated by *Eriogonum ovalifolium* and *Silene acaulis* is also unique and has not been documented in other Idaho alpine studies. Community distribution showed the strongest correlation with exposure, substrate type, and slope. In general, the study area supports fellfield communities that are representative of alpine areas in Idaho and some Great Basin mountain ranges, and dense turflike communities similar to ones found throughout western North America's temperate alpine regions.

Key words: alpine vegetation, Idaho, White Cloud Peaks, multivariate analysis.

While Idaho's alpine flora was largely ignored during the early part of this century, recent studies have documented the existence of well-developed alpine communities in east central Idaho where several mountain ranges reach elevations over 3600 m. Brunsfeld (1981) completed an alpine flora for parts of east central Idaho based on collections from the Lost River and southern Lemhi ranges and the southern Beaverhead Mountains. Caicco (1983) completed the first alpine community study in Idaho working with data from the Pioneer and White Knob Mountains. Moseley (1985) investigated alpine spike-fescue grasslands in portions of east central Idaho, and most recently, Urbanczyk and Henderson (1994) provided a classification and ordination of alpine communities of Sheep Mountain in the Lemhi Range. Together these studies have documented all general alpine community types commonly described for temperate North American mountains (e.g., turf, fellfield, meadow, snowbed, and grassland). These studies refer to arid portions of the climatic spectrum and have been concentrated primarily in regions with carbonate substrates.

The White Cloud Peaks of east central Idaho consist of extremely steep and rugged slopes, providing little opportunity for extensive areas of alpine vegetation to develop. One exception is Railroad Ridge, where gently sloping terrain supports a well-developed expanse of alpine vegetation. In contrast to alpine areas studied to the east, substrates on Railroad Ridge are composed of granitic materials and glacial deposits of argillite and other sedimentary rocks. Because substrate varies within the study area and the White Cloud Peaks receive more precipitation than other alpine areas studied in Idaho, we predicted that Railroad Ridge would support a wide variety of alpine communities, some possibly undescribed for Idaho. To test this prediction, we sampled the alpine vegetation of Railroad Ridge with the objectives of (1) classifying plant communities, (2) associating their distribution with respect to habitat factors such as substrate, moisture, and topographic position, and (3) comparing the vegetation to other alpine vegetation in and beyond Idaho.

STUDY AREA

The study area, located in the Sawtooth National Recreation Area in the northeastern part of the White Cloud Peaks, approximately

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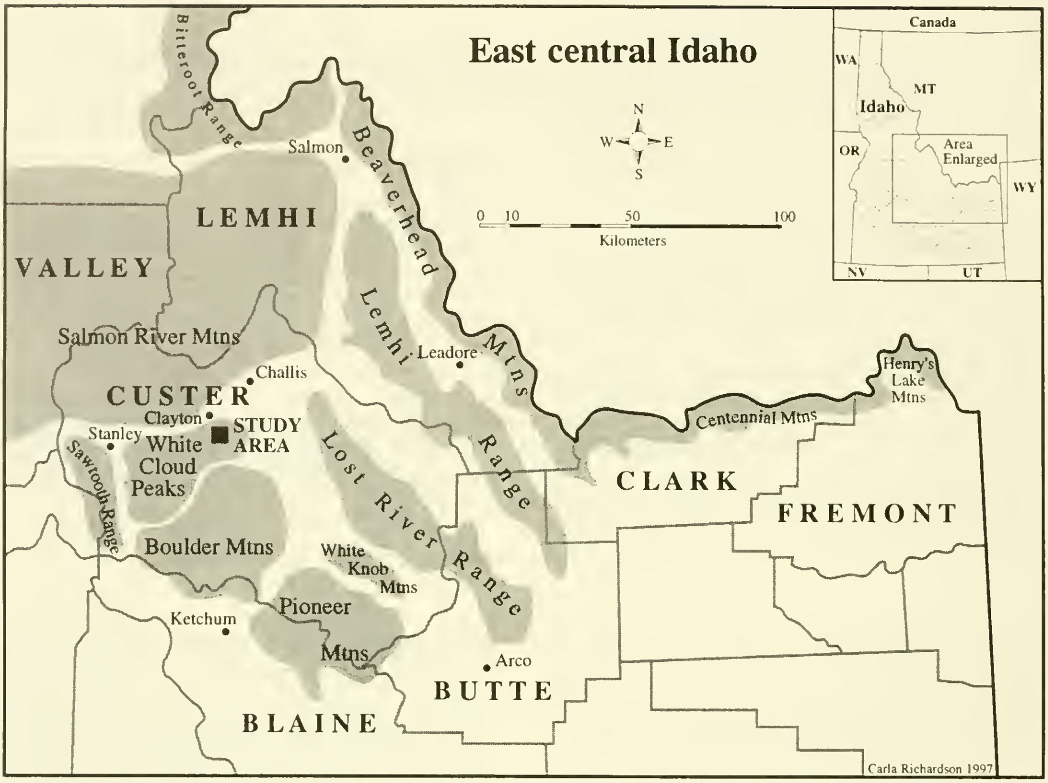
East central Idaho
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Canada
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OR
Area Enlarged
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Bitteroot Range
Salmon
Beaverhead
LEMHI
VALLEY
Lemhi
Mtns
Salmon River Mtns
Challis
Leadore
CUSTER
Clayton
STUDY AREA
Stanley
White Cloud Peaks
Sawtooth Range
Lost River Range
Range
Centennial Mtns
Henry's Lake Mtns
CLARK
FREMONT
Boulder Mtns
White Knob Mtns
Pioneer Mtns
Ketchum
Arco
BUTTE
BLAINE
Carla Richardson 1997

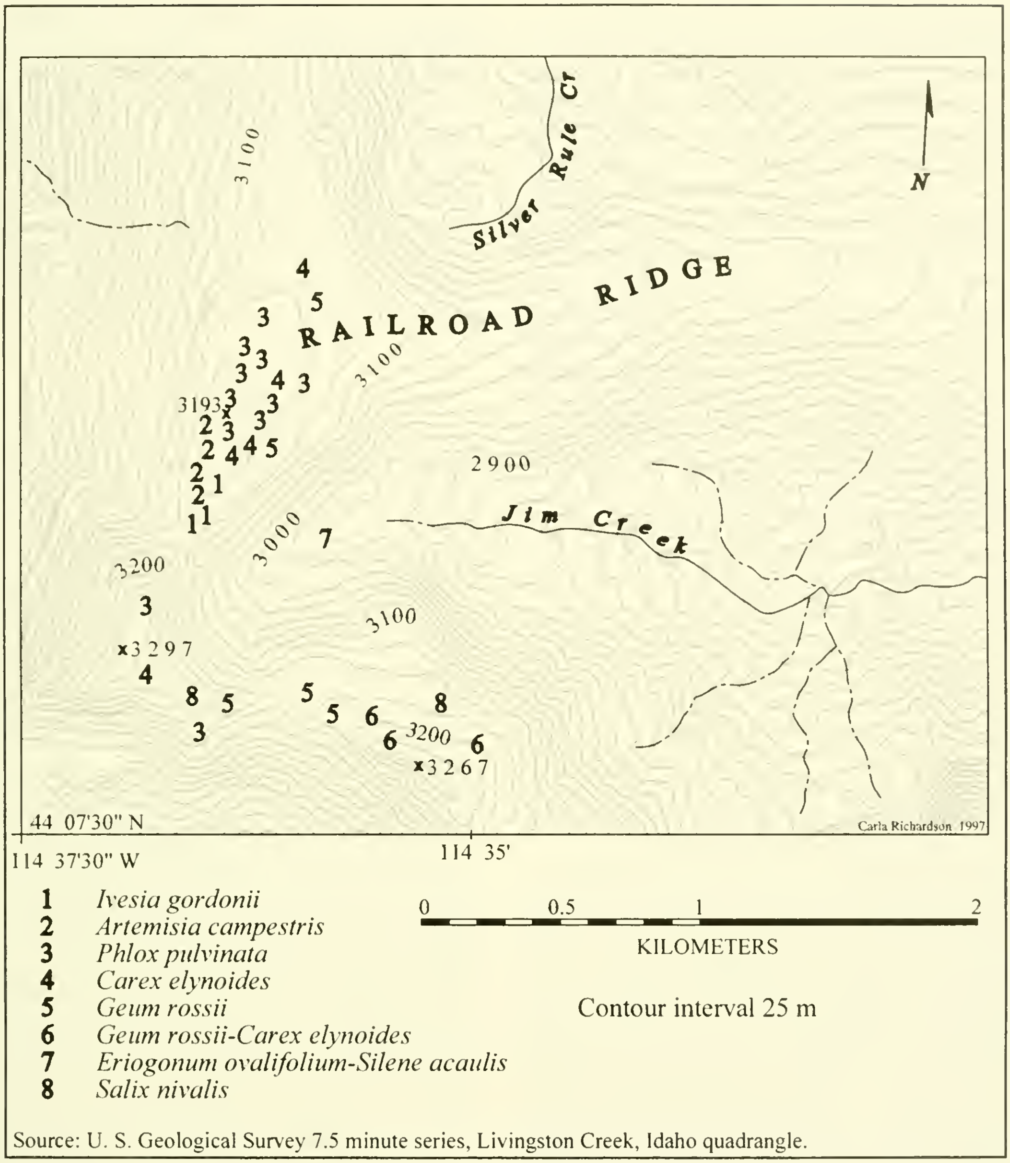
Fig. 1. Location of study area in east central Idaho.

21 km southwest of Clayton, Idaho (44°08′30″N, 114°35′30″W), encompasses 1.4 km of north–south trending ridgeline and 1.3 km of an east–west oriented ridgeline (Fig. 1). Elevation ranges from 2950 to 3297 m. Upper treeline, at approximately 3140 m, is composed of *Pinus albicaulis* mixed with *Abies bifolia, Picea engelmannii, Pinus contorta,* and *Artemisia tridentata.*

Much of Railroad Ridge is covered by unsorted Pleistocene glacial deposits consisting of sedimentary and metasedimentary rocks including siliceous black argillite mixed with occasional fine sandstone and sandy limestone. The northern part of the study area is almost completely capped by gravel-size rocks of this type. Cretaceous intrusive rocks consisting of granite, granodiorite, and aplite are also found in portions of the study area (Zigmont 1982, Fisher et al. 1992).

The coldest months are December and January with a mean temperature of −17°C, while the warmest month is July with a mean temperature of 8°C. Precipitation is approximately 914 mm per year (State Climate Program 1995), most of which falls during winter months as snow, although high-altitude convectional storms are also important during late spring and summer. In general, the study area has a montane climate subject to both maritime and continental influences that result in cold, wet winters and warm, dry summers (Ross and Savage 1967).

Land-use history included mining until the Sawtooth National Recreation Area was established in 1972. Scars from mining operations, though evident, are localized in extent. Grazing by livestock dates back to around 1900, alternating between sheep and cattle up to the present (Seth Phalen, Stanley Ranger Station, personal communication). We conjecture that the most inaccessible portions of the study area were subjected only to light grazing, while the more accessible areas were probably heavily grazed during at least the 1st half of this century. The area is currently grazed by cattle, but none were observed in the alpine zone during this study.


Silver Rule Cr
N
RAILROAD RIDGE
3100
3193
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Jim Creek
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3297
3267
44 07'30" N
114 37'30" W
114 35'
Carla Richardson 1997
1 Ivesia gordonii
2 Artemisia campestris
3 Phlox pulvinata
4 Carex elynoides
5 Geum rossii
6 Geum rossii-Carex elynoides
7 Eriogonum ovalifolium-Silene acaulis
8 Salix nivalis
0 0.5 1 2
KILOMETERS
Contour interval 25 m

Source: U. S. Geological Survey 7.5 minute series, Livingston Creek, Idaho quadrangle.

Fig. 2. Location of stands sampled on Railroad Ridge and their community membership.

METHODS

Data Collection

Fieldwork was conducted 12 July–15 August 1994 and completed 4–9 August 1995. Only vegetation above upper treeline and the zone of woody *Artemisia* species, which extended approximately 50 m beyond upper treeline, was examined. Sixty-nine plots were sampled using the methods of Bliss (1963) and Urbanczyk and Henderson (1994). Forty-three of 69 plots sampled were located on the northern portion of Railroad Ridge, 24 plots were placed to the south on an east–west trending ridgeline, and the remaining 2 were situated in the drainage between the 2 main ridges (Fig. 2).

Plots were not established in ecotonal areas or highly disturbed locations, but within homogeneous stands of plants at least 60 m^2 in size. Talus and boulder field habitats were not sampled. Criteria used for stand selection included uniformity in substrate type, moisture status, disturbance, and species composition and cover. Within each stand, we established 1 or more 4 × 8-m plots and then divided them into 8 rows, each 4 × 1 m. Four rows were randomly selected for sampling. In each selected row, 5 sampling quadrats, each 0.2 × 0.5 m, were spaced at .5-m intervals. If an odd-numbered row was selected to be sampled, we placed the 1st quadrat adjacent to the edge of the plot. If an even-numbered row was selected, the 1st quadrat was displaced by .5 m. This resulted in 20 quadrats with a total sampling area of 2 m^2. Using the canopy-coverage method of Daubenmire (1959) and Urbanczyk and Henderson (1994), we estimated percent crown cover for all species in each quadrat. Plot cover for a species was the average of the 20 quadrats. Total vegetation cover was calculated by subtracting bare ground and rock cover values from 100. Due to overlap in canopies of different species, total percent cover for a quadrat is not expected to equal 100%, and total vegetation cover is not expected to equal the sum of the individual species' cover values. Percent frequency of presence in the plots of each species was also recorded.

For each plot we recorded the following habitat information: exact location on a topographic map, elevation, aspect, slope, substrate, and exposure index. Elevation was taken from the U.S. Geological Survey Livingston Creek, Idaho 7.5′ Quadrangle. Aspect and slope were measured by a Brunton compass and clinometer, respectively. Substrate was ascertained by rock samples identified by William Rember (Department of Geology, University of Idaho). Exposure index was estimated on a scale of 1 to 5, with 1 being the lowest exposure, and reflected several environmental factors simultaneously (Del Moral 1979). The index was used as a measure of moisture status of the sampled plots in relation to each other. Factors considered when assigning the index to a plot were aspect and slope, topographic position, substrate, soil development and texture, and snowmelt/drainage patterns.

Voucher specimens of all plant species were collected and deposited in the University of Idaho Vascular Herbarium (ID). Nomenclature follows Hitchcock and Cronquist (1973) except for the Poaceae (Welsh et al. 1987) and Pinaceae (Flora of North America Editorial Committee 1993).

Climatic data were estimated from regional weather stations and precipitation maps for Idaho. Temperature information originated from weather station data from Challis, Idaho, elevation 1546 m, 51 km northeast, and from Stanley, Idaho, elevation 1952 m, 29 km northwest, and was corrected for elevation (0.63°C/100 m; Myron Molnau, Office of State Climatologist, personal communication).

Data Analysis

All data were analyzed by statistical computer programs in the Cornell Ecology series. TWINSPAN (Hill 1979) provided a classification, and canonical correspondence analysis (CCA), using the program CANOCO (Ter Braak 1987–1992), provided ordinations. Only 43 species with at least 1% cover in ≥1 plots were used in the analyses (see Appendix). Deletion of rare species, as suggested by Gauch (1982), was attempted but had no effect on the general interpretation of results. The complete data set was retained for analysis except in a 2nd ordination where deleting 2 extreme, outlying plots facilitated a better interpretation of the remaining plots.

TWINSPAN is a hierarchical classification program that uses reciprocal averaging repeatedly to divide the data set into progressively smaller groups (Hill 1979). Analysis was accomplished with all default values in place, except that the maximum number of divisions was limited to 5. Percent-cover data were transformed using default species cut levels, which de-emphasize abundant species, allowing less abundant species to have more influence in the classification. The resulting dendrogram was interpreted with respect to environmental factors and field observations with the communities ultimately being derived from several levels in the hierarchy.

Species percent-cover values were transformed to the Octave Scale (Gauch 1982) for the CCA analysis. CCA uses reciprocal averaging constrained by environmental information (Ter Braak 1987–1992). Axes of the ordination diagram are linear combinations of measured environmental variables (i.e., elevation, slope, aspect, substrate, and moisture status). Each axis has an eigenvalue (e), which is a measure of variation of the species data explained by that axis. Larger eigenvalues correspond to a larger dispersion of species scores along the axis. Each environmental variable also has a correlation coefficient (*r*) for each axis, which indicates numerically how well that environmental variable helps explain observed variation on the axis. Total variation explained by the ordination is determined by adding eigenvalues for the axes and then dividing by the total of the constrained eigenvalues (Gauch 1982).

RESULTS

Classification

TWINSPAN analysis of the data suggested 8 groupings that are shown in Table 1 and the resulting dendrogram (Fig. 3). The 1st division of the dendrogram (e = 0.597) reflected a general shift from the lower-elevation sites on the north ridge (left side of dendrogram) to those sampled in the higher-altitude, southern portion of the study area (right). The 2nd division (e = 0.393) distinguished the more unique, but less extensive, *Ivesia gordonii* and *Artemisia campestris* communities (left) from the expansive and ubiquitous *Phlox pulvinata* and *Carex elynoides* communities (right). Division 3 (e = 0.384) separated the *Salix nivalis* community (right) from the rest (left). The 6th division (e = 0.375) separated turf communities (left) from those dominated primarily by cushion plants (right). Division 7 (e = 0.363) was associated with a moisture gradient and separated communities with higher exposure (right) from the *Geum rossii* community (left), which occupies more mesic habitats. Divisions 8 (e = 0.464) and 10 (e = 0.510) further differentiated fellfield and turf communities.

Ivesia gordonii (group 1, *n* = 5 plots) dominated a small number of fellfield communities near the southern saddle on Railroad Ridge's north flank (Fig. 2). These stands were found on gravelly, glacial deposits of sedimentary rocks with poor to moderately developed soils (slope 7°). They occurred on southeast- and west-facing slopes at an average elevation of 3129 m. Average exposure index was 3.1. Total vegetation cover was 47% with *Ivesia gordonii* at 30%. Other species in this community included *Oxytropis campestris* (7.8%), *Artemisia campestris* (7.4%), *Draba densifolia* (2.4%), *Agoseris glauca* (2.3%), and *Phlox pulvinata* (1.5%).

The *Artemisia campestris* community (group 2, *n* = 7 plots) occupied mainly southwest aspects of moderately steep slopes (10°) at an average elevation of 3155 m. It was found only on sedimentary deposits with shallow, rocky, poorly developed soils (exposure index = 4.3). Total vegetation cover was 34% with *Artemisia campestris* accounting for 19.1%. *Oxytropis campestris* was also a significant component with 5.3% cover, as well as *Draba densifolia* (3.3%), *Phlox pulvinata* (3%), *Eriogonum ovalifolium* (2.4%), *Agoseris glauca* (2%), and *Poa fendleriana* (1.5%).

The *Phlox pulvinata* community (group 3, *n* = 23 plots) was sampled primarily on sedimentary deposits, but also occasionally on mixed substrate. Sites ranged from nearly flat (1°) to steep (18°) and occurred on a variety of aspects (northwest, north, northeast, southeast, and south). The exposure index ranged from 2.5 to 5.0, with an average value of 3.4. Sampling elevation was 3155–3267 m. Total vegetation cover was 54% with *Phlox pulvinata* accounting for 25%. Other important components were *Agoseris glauca* (7.1%), *Poa glauca* (6.2%), *Elymus elymoides* (5.5%), *Oxytropis campestris* (3.9%), *Artemisia campestris* (3.5%), and *Potentilla diversifolia* (2.2%).

Carex elynoides forms a dense turf community (group 4, *n* = 10 plots) common in the study area. Total vegetation cover was 76.4% with *Carex elynoides* at 68.5%. Few other species were present in this community except *Phlox pulvinata* (12.3%) and *Agoseris glauca* (8%), which were constants. This community was observed primarily on sedimentary deposits with southeast aspects, except for 1 stand on granite with a north aspect. Sampling elevation was 3146–3261 m on gently sloping terrain (5.1°), with an average exposure index of 2.9.

Geum rossii forms a turf community (group 5, *n* = 12 plots) also common in the study area. It was sampled on all substrate types with mostly gentle slopes (6.2° average), but occasionally steep (18°). This community was observed on north, northwest, and southeast aspects at an average elevation of 3172 m. The average exposure index was 2.6. Total vegetation cover was 56.7% with *Geum rossii* at 33.8%. Other species present included *Ivesia gordonii* (6.0%), *Potentilla diversifolia* (5.4%), *Phlox pulvinata* (4%), *Carex elynoides* (2.8%),

TABLE 1. Community group composition with only the 43 species used in the data analysis included. The 8 community groups are as follows: (1) *Ivesia gordonii*, (2) *Artemisia campestris*, (3) *Phlox pulvinata*, (4) *Carex elynoides*, (5) *Geum rossii*, (6) *Geum rossii–Carex elynoides*, (7) *Eriogonum ovalifolium–Silene acaulis*, and (8) *Salix nivalis*. Mean percent cover (C) and frequency of presence in plots (F) are given for each species. Cover less than 0.5% is indicated by *.

	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7		Group 8	
Species	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Agoseris glauca	2.3	60	2.0	71	7.1	78	8.0	100	*	50	*	50				
Androsace septentrionalis	*	80	0.7	100	0.7	70	*	10	*	33	*	33	*	50		
Antennaria umbrinella					*	8	*	10	*	33	*	33	*	50	1.4	50
Arenaria congesta			*	14	0.5	8	1.3	50	2.2	33	1.5	100			0.5	50
Arenaria obtusiloba					0.5	17	*	20	1.2	33	*	17	1.3	50	1.5	50
Artemisia campestris	7.4	100	19.1	100	3.5	61	0.7	70	*	8						
Aster alpigenus									0.7	25					*	50
Astragalus kentrophyta	*	40	*	14	*	13										
Bupleurum americanum	*	40	*	57	0.7	78	*	30	0.5	50	1.3	100				
Carex elynoides					*	13	68.5	100	2.8	58	31.5	100			3.5	50
Carex phaeocephala									*	50	*	33				
Draba densifolia	2.4	100	3.3	86	1.6	65	*	20	*	58	*	67	*	50	*	25
Elymus elymoides			*	14	5.2	96	1.0	60			1.0	67				
Erigeron compositus	*	40	*	43	*	8	*	10					*	50		
Erigeron simplex									0.6	17	*	17			*	25
Eriogonum flavum	*	20													*	25
Eriogonum ovalifolium	0.5	100	2.4	100	1.3	65	*	30	*	17			5.8	100		
Eritrichium nanum					*	8			*	42					*	50
Festuca ovina brevifolia					*	39	*	30	2.3	92	3.1	100	1.6	100	1.5	100
Festuca ovina ingrata									0.8	25						
Geum rossii					*	4	*	30	33.8	100	36.3	100	2.7	100	3.6	50

TABLE 1. Continued.

	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Group 7		Group 8	
Species	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Haplopappus lanuginosus	*	100	0.5	100	*	13			*	50	*	50			*	50
Hymenoxys grandiflora					1.6	39	*	10	*	17						
Ivesia gordonii	29.8	100	*	29	1.1	30	*	30	6.0	67			5.0	100	*	50
Lomatium foeniculaceum	*	100	0.6	86	1.1	78	*	50								
Lupinus argenteus					1.5	39			0.9	42						
Luzula spicata									*	25			0.8	100	*	50
Oxytropis campestris	7.8	100	5.3	100	3.9	83	2.0	80	*	17						
Oxytropis viscida					0.6	17	0.7	20	1.4	50	1.4	67			1.3	50
Penstemon procerus					*	8			*	17						
Phlox pulvinata	1.5	100	3.0	100	25.0	100	12.3	100	4.0	100	4.3	100	3.4	100	*	25
Poa fendleriana	0.7	100	1.5	100	1.4	70	0.9	80	*	17			*	50		
Poa glauca rupicola	*	40	0.8	72	6.2	87	1.7	100	0.9	100	1.6	100	*	50	2.1	100
Poa secunda	*				0.5	8										
Potentilla diversifolia					1.8	17	*	20	5.4	50	1.5	33			4.0	50
Potentilla ovina	*	20	*	14	2.2	48	2.0	90			*	33				
Salix nivalis											*	17			26.8	100
Sedum lanceolatum					*	8			*	33	*	67	*	50	*	50
Selaginella densa					0.6	17	*	20			2.7	100	2.9	100	1.2	50
Silene acaulis									*	8			5.7	100		
Silene repens	*	80	*	14	0.5	13	*	10								
Smelowskia calycina					*	13					*	33			*	25
Trisetum spicatum			*	14	0.6	17	*	30	0.5	67	*	50	*	50	2.0	75

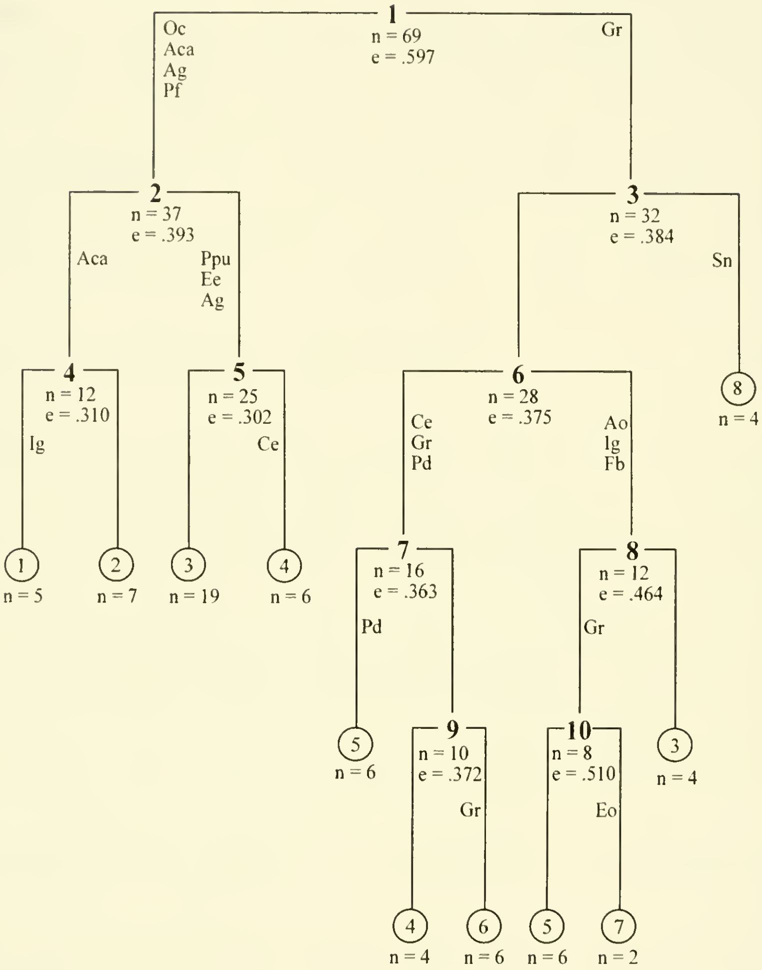

Fig. 3. TWINSPAN dendrogram. Large boldface numbers are division numbers referred to in text. Number of plots (*n*) prior to division and the eigenvalue (e) associated with that division are directly below the division number. TWINSPAN indicator species, species that are preferential to 1 side of the dichotomy, are shown for each division. Unlabeled branches on the dendrogram occur when only 1 indicator species was used for a particular division. Species abbreviations are explained in the Appendix. Circled numbers refer to communities discussed in the text: (1) *Ivesia gordonii*, (2) *Artemisia campestris*, (3) *Phlox pulvinata*, (4) *Carex elynoides*, (5) *Geum rossii*, (6) *Geum rossii–Carex elynoides*, (7) *Eriogonum ovalifolium–Silene acaulis*, and (8) *Salix nivalis*.

Festuca ovina var. *brevifolia* (2.3%), and *Arenaria obtusiloba* (1.7%).

Geum rossii and *Carex elynoides* co-dominated a small group of stands (group 6, *n* = 6 plots) on Railroad Ridge. Total vegetation cover was high (67%) with *Geum rossii* (36.3%) cover averaging slightly more than *Carex elynoides* (31.5%). Many other species were sampled in this community including *Phlox pulvinata* (4.3%), *Festuca ovina* var. *brevifolia* (3.1%), *Selaginella densa* (2.7%), *Poa glauca* (1.6%), *Arenaria congesta* (1.5%), *Potentilla diversifolia* (1.5%), and *Oxytropis viscida* (1.4%). Occurring mostly on granite, this community also occurred occasionally on mixed substrates with moderately developed soils. Slopes were steep (17°) on northeast and northwest aspects at high elevations (3209 m), with an average exposure index of 3.3.

The *Eriogonum ovalifolium–Silene acaulis* cushion plant community (group 7, *n* = 2 plots) was the lowest elevation site sampled (2957 m). It was located on colluvial deposits of granitic materials at the bottom of the drainage separating the 2 main ridges of the study area (Fig. 2). Soil development was poor on a southwest aspect (slope 10°), with an exposure index of 4.0. Total vegetation cover was low (25.6%) with *Eriogonum ovalifolium* (5.8%) and *Silene acaulis* (5.7%) having nearly equivalent coverage. *Ivesia gordonii*, with 5% coverage, was also an important component. Other species sampled included *Phlox pulvinata* (3.4%), *Selaginella densa* (2.9%), *Geum rossii* (2.7%), *Festuca ovina* var. *brevifolia* (1.6%), and *Arenaria obtusiloba* (1.3%).

The *Salix nivalis* community (group 8, *n* = 4 plots) was represented by 2 stands in which *Salix nivalis* was the predominant species. One stand was located on a shelf (slope 5°) at the base of a steep ridge, the other on a moderately steep, gravelly slope (8.5°; Fig. 2). Both sites were sheltered from prevailing westerly winds due to a northwest or northeast aspect (exposure index = 2.3). They occurred only on granite at higher elevations (3200 m). Soil development was moderate on the steeper site but well developed on the other, more gently sloped stand. At 26.8% cover, *Salix nivalis* accounted for more than half the total vegetation cover (43.9%). Other important species present were *Potentilla diversifolia* (4%), *Geum rossii* (3.6%), *Carex elynoides* (3.5%), *Poa glauca* (2.1%), and *Trisetum spicatum* (2%).

Ordination

An initial ordination with the entire data set highlighted the *Eriogonum ovalifolium–Silene acaulis* community as distinct from the remaining plots. Plots in this community were among the lowest elevation sites sampled but had a high exposure index. Outliers such as this can obscure the ordination by occupying an extreme position on 1 axis, resulting in the compression of the remaining groups (Hill 1979, Gauch 1982). To address this, we performed a 2nd ordination with the *Eriogonum ovalifolium–Silene acaulis* plots deleted (Fig. 4). Greater separation of the remaining plots was achieved, and this facilitated a better interpretation of those communities.

The 1st axis in the ordination was correlated with substrate ($r = 0.5$) and elevation ($r = 0.6$), while the 2nd axis was correlated with exposure index ($r = 0.7$) and slope ($r = 0.6$). The 3rd axis was correlated primarily with substrate ($r = 0.3$). Utilizing the first 2 axes, the species and plot ordination diagrams display 64% and 71% of the total variation, respectively, in all axes of the CCA ordination.

Plot ordination (Fig. 4) positioned *Salix nivalis* plots in locations denoting low exposure and a propensity for growing on granitic substrates. *Artemisia campestris* plots were located in positions indicating higher exposure and an affinity for sedimentary substrates. The remaining groups were distributed in between and were further differentiated by substrate, slope, and elevation. *Carex elynoides* community plots were dispersed across the diagram. *Geum rossii* plots spanned nearly the entire length of the 2nd axis, across a wide range of slope and exposure values, but were more constricted along the 1st axis, reflecting a preference for granite substrates and higher elevations.

Species ordination also reflected an exposure gradient (Fig. 5). The 1st species ordination with the entire data set (not shown) placed *Silene acaulis* in the most exposed position and *Salix nivalis* in a more mesic position. The remaining species were compressed in the center of the diagram. Deletion of group 7 plots (*Eriogonum ovalifolium–Silene acaulis* community) from a 2nd ordination resulted in greater separation of the species since *Silene acaulis* was sampled only within group 7 plots (Fig. 5).

Penstemon procerus var. *procerus* and *Erigeron compositus* var. *glabratus* were located in positions indicating high exposure. *Aster alpigenus, Luzula spicata, Festuca ovina* var. *ingrata, Erigeron simplex*, and *Salix nivalis* all occupied the portion of the diagram indicating least exposed sites. *Oxytropis viscida, Selaginella densa*, and *Arenaria obtusiloba* were the highest elevation species collected, while at the opposite extreme was an assemblage of many species including *Artemisia campestris, Eriogonum ovalifolium* var. *depressum*, and *Oxytropis campestris* var. *cusickii*. Several species, including *Artemisia campestris, Oxytropis campestris*, and *Erigeron compositus*, were collected only on sedimentary substrate. *Salix nivalis* and *Oxytropis viscida* were the only species restricted to granite.

DISCUSSION

Railroad Ridge's alpine communities were distinguished from one another by their physiognomy and species composition, and along environmental gradients such as elevation, slope, exposure, and substrate type. Alpine

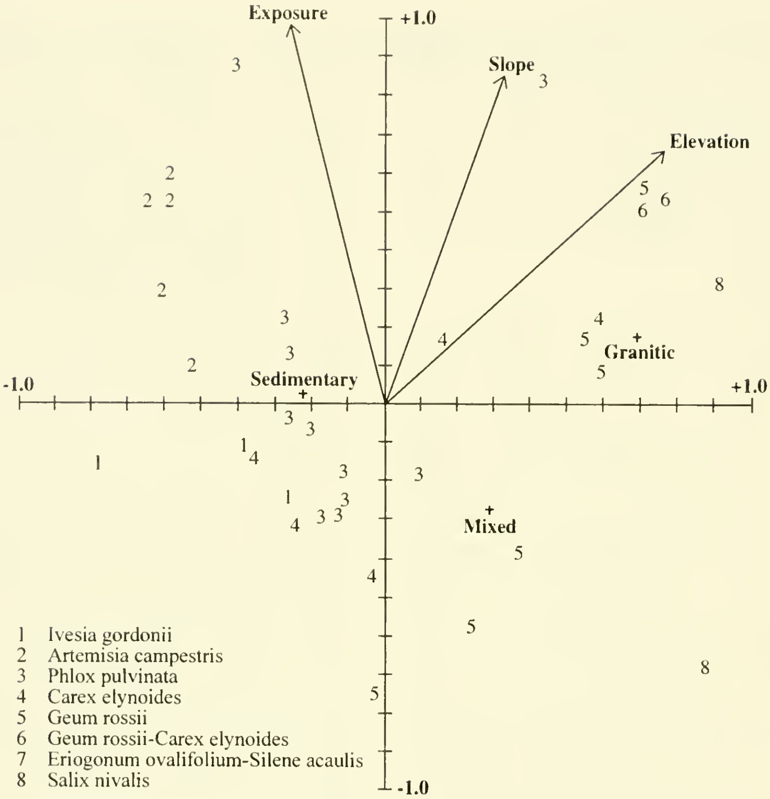

Fig. 4. CCA ordination of plots with group 7 (*Eriogonum ovalifolium–Silene acaulis*) plots deleted. Numbers indicate community membership. Substrate classes are indicated by sedimentary, granitic, and mixed, which includes both sedimentary and granitic parent materials.

fellfield communities were well represented in the study area and were usually dominated by cushion plants such as *Phlox pulvinata* or *Ivesia gordonii.* Fellfields are distinguished from talus or boulder fields in that the former occur on ridgetops and gentle slopes, and underlying rocks are stabilized, not shifting. *Ivesia gordonii* and *Artemisia campestris* fellfields were among the first communities to separate in the classification. In the dendrogram (Fig. 3), group 1 (*Ivesia gordonii*) initially remained with group 2 (*Artemisia campestris*), but the 2 were separated at division 4 due to the conspicuous absence of *Ivesia gordonii* in group 2. The 2 communities were located in adjacent areas but with differing environmental conditions. *Ivesia gordonii* fellfields occupied moderate slopes on mainly southeast aspects where winter snow accumulation can occur, resulting in lower exposure and higher total vegetation cover than the *Artemisia campestris* stands. The absence of *Ivesia gordonii* from group 2 may reflect a shift from mesic sites with lower exposure to drier, more exposed locations. CCA plot ordination (Fig. 4) also reflected exposure gradient, locating *Ivesia gordonii* plots in a more mesic position on the diagram. Species ordination (Fig. 5) placed *Ivesia gordonii* near the center of the diagram, reflecting an average habitat preference.

Ivesia gordonii is found primarily in the central Rocky Mountains and westward into the mountain ranges of the Great Basin and California (Hitchcock and Cronquist 1973). *Ivesia gordonii*–dominated fellfields are uncommon, previously known in Idaho only from the Pioneer Mountains (Caicco 1983). Fellfields in that study area occupied similar habitats along ridgetops at moderate elevations with poorly developed soils, but were underlain by different substrates (quartz monzonite and Challis volcanics). Beyond Idaho, *Ivesia gordonii*–dominated fellfields have been reported from the Ruby Range in the West Elk Mountains,

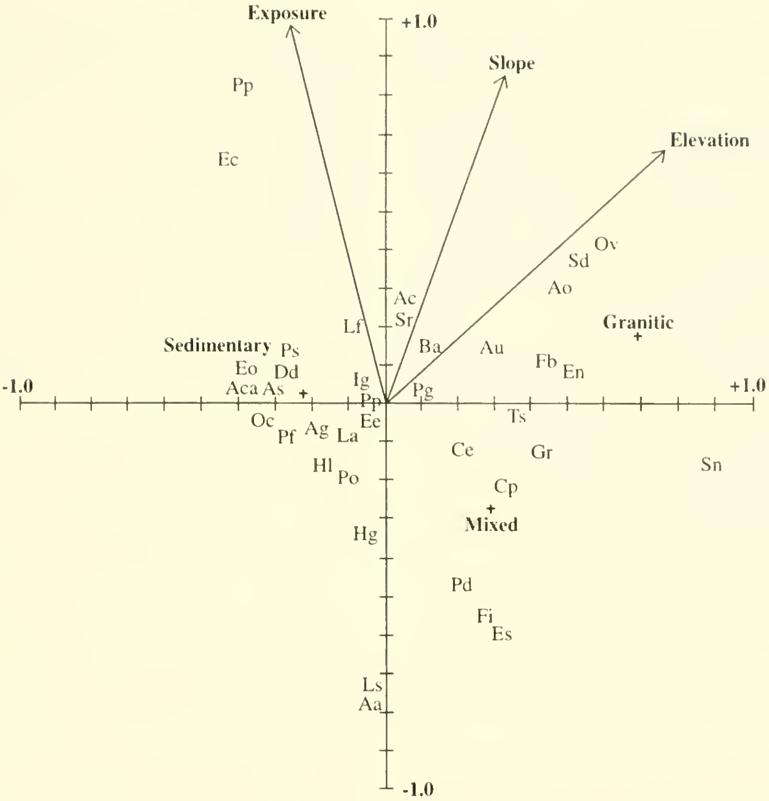

Fig. 5. CCA ordination of species with group 7 (*Eriogonum ovalifolium–Silene acaulis*) plots deleted. Species abbreviations are listed in the Appendix. Substrate classes are indicated by sedimentary, granitic, and mixed, which includes both sedimentary and granitic parent materials.

Colorado (Hartman and Rottman 1987), where they are restricted to ridgetops or bedrock outcrops. Ellison (1954) described an alpine relic community located in the subalpine zone on the Wasatch Plateau, Utah, dominated by *Ivesia gordonii*, and Taye (1995) reported a gravelly barren community in the Tushar Mountains, Utah, where *Ivesia gordonii* was among the most important inhabitants.

Group 2 (*Artemisia campestris*) plots occupied positions on the ordination (Fig. 4) indicating high exposure and restriction to sedimentary substrates. Species ordination (Fig. 5) placed *Artemisia campestris* in a moderate exposure position at lower-elevation sites with moderately steep slopes, and only on sedimentary rocks. *Artemisia campestris* is a widespread, circumboreal taxon that extends south in North America to Oregon, Arizona, Michigan, and Vermont. It ranges from the high mountains of northern Washington to northern Montana and Colorado (Hitchcock and Cronquist 1973) but is known in Idaho only from the White Cloud Peaks. No communities dominated by or containing this species have been described previously in Idaho. *Artemisia campestris* ssp. *borealis* var. *borealis* has been reported in the Sawatch and Front ranges of Colorado as occasional on xeric slopes and rock-predominating habitats but is not mentioned as a community dominant (Komarkova 1979, Hartman and Rottman 1988). In general, it is found in low abundance in dry meadows and rocky areas throughout the mountains of western North America (Johnson and Billings 1962, Major and Taylor 1977, Spence and Shaw 1981, Hartman and Rottmann 1985).

Group 3 (*Phlox pulvinata*) was the predominant fellfield type at Railroad Ridge. The classification (Fig. 3) highlighted 2 distinct phases of the *Phlox pulvinata* community that were separated at division 1 due to the absence of several key species (*Agoseris glauca, Artemisia campestris*, and *Oxytropis campestris*) from 1 group. CCA plot ordination (Fig. 4) also recognized the 2 phases of this community as distinct. One group of plots was located near the diagram center, showing a general habitat preference for moderate slopes at medium elevation ranges and moderate exposures. The other plots were positioned indicating very high exposure, with steep slopes at high elevations. Species ordination (Fig. 5) placed *Phlox pulvinata* at the center of the diagram, reflecting its generalized habitat preferences.

Phlox pulvinata is found in open, rocky places at moderate to high elevations in the northern Rockies and mountain ranges of the Great Basin (Hitchcock and Cronquist 1973). Fellfields of the White Knob Mountains in Idaho are dominated by *Phlox pulvinata* and occupy a similar range of environmental conditions (Caicco 1983). Beyond Idaho, *Phlox pulvinata* has been documented from similar habitats in some Great Basin mountain ranges (e.g., Tushar Mountains, Utah; Taye 1995) and on exposed gravel and scree slopes in the northern Rocky Mountains, Montana (Bamberg and Major 1968).

The turf community is a dry, meadowlike habitat occupying a major part of Railroad Ridge. In general, soil development is extensive and plant cover complete, with the exceptions of rock outcrops and areas of disturbance. Floristic diversity is generally low, possibly due to competitive exclusion. Turf communities in the study area are dominated by either *Carex elynoides* or *Geum rossii*, or both. The 1st turf community to be distinguished in the classification (Fig. 3) was *Carex elynoides* (group 4). Two phases of *Carex elynoides* turf were identified and separated early at division 1 (e = .597) due to the low cover value (1.8%) of *Agoseris glauca* in 1 group of plots. CCA plot ordination (Fig. 4) failed to separate these 2 phases. All plots were scattered but generally remained near the center of the diagram, reflecting more generalized habitat preferences.

Carex elynoides–dominated turf is common in east central Idaho where it occurs on lower alpine slopes and exposed ridges. It has been documented throughout east central Idaho on both calcareous and siliceous substrates (Caicco 1983, Moseley 1985, Urbanczyk and Henderson 1994). Although varying in species composition, this widely distributed community is usually characterized by a sedge mat of nearly complete cover with *Phlox pulvinata* as a constant in the forb layer. *Carex elynoides* is common above treeline from southwestern Montana to Colorado, west to Utah and Nevada (Hitchcock and Cronquist 1973), and has been reported as a turf community from alpine areas throughout the southern and central Rocky Mountains (Bamberg and Major 1968, Komarkova 1979) and the Great Basin mountain ranges (Loope 1969, Taye 1995). Its habitat has been characterized as warm, dry, southern aspects that are snow covered in winter (Komarkova 1979). Our observations generally agree with this, but in our study area we occasionally encountered other aspects.

The classification (Fig. 3) also highlighted 2 phases of *Geum rossii*–dominated turf (group 5) that were separated at division 6 because of the presence of *Potentilla diversifolia* in the 1st group and *Arenaria obtusiloba* and *Ivesia gordonii* in the 2nd group. In CCA plot ordination (Fig. 4), the 1st group of plots occupied positions indicating a mesic habitat on mixed or sedimentary substrates; the 2nd group of plots occupied positions reflecting more exposed conditions at higher elevations and primarily on granitic substrates.

Geum rossii inhabits alpine talus, cirques, and wind-swept ridges of the central and southern Rocky Mountains, west into the Cascades of Oregon and Washington (Hitchcock and Cronquist 1973). Abundant in xeric alpine meadows in the Rocky Mountains, it reaches its optimum in shallow depressions with moderately prolonged snow cover. *Geum rossii* is common in the Colorado Rocky Mountains and extends south to San Francisco Mountain, Arizona (Komarkova 1979, Schaack 1983, Hartman and Rottman 1987). It dominates dry to mesic meadows in the northern Rocky Mountains in Montana, Tushar Mountains, Utah, and North Ruby Mountains, Nevada (Bamberg and Major 1968, Loope 1969, Taye 1995). Brunsfeld (1981) suggested *Geum rossii* turf to be the most characteristic community type on level quartzitic substrates in east central Idaho, yet this is the 1st study of Idaho alpine to sample and document it. This community type is apparently absent from the nearby Pioneer and White Knob Mountains (Caicco 1983) and was not observed on Sheep Mountain in the Lemhi Range (Urbanczyk and Henderson 1994). These areas, however, have primarily carbonate substrates.

Another turf community at Railroad Ridge is co-dominated by *Geum rossii* and *Carex elynoides* and, as indicated by the dendrogram (Fig. 3), is similar to groups 4 (*Carex elynoides*) and 5 (*Geum rossii*). It separated from group 5 plots at division 7 due to the low coverage of *Potentilla diversifolia.* At division 9 it separated from group 4 because of the high percentage of *Geum rossii.* The CCA ordination diagram (Fig. 4) shows that this community was represented by some of the highest elevation sites and steepest slopes sampled. Species and plot ordinations (Figs. 4, 5) show *Carex elynoides* reaching optimum cover on sedimentary substrates, while *Geum rossii* is found primarily on granitic substrates. Brunsfeld (1981) observed that *Geum rossii* is found primarily on quartzitic substrates, while *Carex elynoides* has been documented on nearly all substrates in east central Idaho.

Turf communities co-dominated by *Geum rossii* and *Carex elynoides* have not been described for Idaho. Hartman and Rottman (1985) described a dry, southeast-facing meadow in the San Juan Mountains, Colorado, dominated by *Geum rossii*, *Carex elynoides*, and *Hymenoxys grandiflora.* Briggs and MacMahon (1982) described a similar *Geum*-sedge community in the Uinta Mountains, Utah, but the dominant sedge was *Carex rupestris* rather than *Carex elynoides*. Another *Geum*-sedge community is common on the Beartooth Plateau, Montana, where a continuum from *Geum rossii* to *Carex drummondiana* dominance can be observed (Johnson and Billings 1962).

The *Eriogonum ovalifolium–Silene acaulis* community (group 7) was highlighted by the 1st CCA plot ordination (not shown) as unique among the groups. Its place on the diagram indicated high exposure. Identified as an outlier, it was subsequently deleted from the ordination to facilitate better interpretation of the other groups. In the 1st species ordination (not shown), *Silene acaulis* was also highlighted as an outlier in an extremely exposed position on the diagram and was subsequently deleted. The 2nd species ordination (Fig. 5) placed *Eriogonum ovalifolium* in a moderately exposed position at lower elevations with a preference for sedimentary substrates. In the dendrogram (Fig. 3), group 7 initially branched with group 5 (*Geum rossii*), but was separated at division 10 due to absence of *Eriogonum ovalifolium* in group 5.

Eriogonum ovalifolium is found chiefly in Montana and Idaho, north to the Canadian Rockies, and west to Oregon (Hitchcock and Cronquist 1973). It is common on all substrates on rocky ridges and stable talus throughout east central Idaho. Moseley (1985) described a community in east central Idaho characterized by increased amounts of exposed rock where *Eriogonum ovalifolium* and *Ivesia gordonii* were important; there is no mention of *Silene acaulis* as an important component, however. *Eriogonum ovalifolium* also inhabits debris accumulations in the Teton Range, Wyoming (Spence and Shaw 1981), but again, not with *Silene acaulis.*

Silene acaulis is a widespread, circumpolar species entending south into the high mountains of western North America (Hitchcock and Cronquist 1973). Common on non-calcareous substrates in east central Idaho, it has not been documented previously as an important community component. *Silene acaulis* has been reported from the North Ruby Mountains, Nevada, where it is abundant with *Phlox pulvinata* in alpine cirques (Loope 1969). It is also a conspicuous member of communities in the Uinta Mountains, Utah, and central Rocky Mountains, south to San Francisco Peak, Arizona, but not in association with *Eriogonum ovalifolium* (Hayward 1952, Komarkova and Webber 1978, Schaak 1983, Hartman and Rottman 1985).

The *Salix nivalis* community (group 8) separated early at division 3 in the dendrogram (Fig. 3) with *Salix nivalis* as the indicator species. CCA ordination also highlighted this community as distinct from the rest. Snowbed communities usually occur in depressed areas with poor drainage, below snowdrifts, and occasionally below talus or boulder fields, but generally they are not well represented in the study area. *Salix nivalis* occupies moist to mesic sites and in the study area was found only on granite, although it has been collected elsewhere in east central Idaho on other substrates. Species ordination (Fig. 5) placed *Salix nivalis* in the lower right position, denoting a mesic habitat found only on granite.

Salix nivalis communities are common in moist alpine habitats of east central Idaho. This community type has been documented in the Lemhi Range on dolomite substrate in association with persistent snowbanks (Urbanczyk and Henderson 1994). *Salix nivalis* also has been observed forming extensive mats in other parts of east central Idaho (Brunsfeld 1981), but it is apparently replaced by *Salix arctica* in the Pioneer Mountains (Caicco 1983). It inhabits meadows, talus slopes, and rocky ledges at and above treeline in the mountains of southern British Columbia and Alberta to California, Nevada, Utah, and New Mexico (Hitchcock and Cronquist 1973). It dominates cool, mesic to subhygric alpine meadows throughout the mountains of western North America, including the Front Range, Colorado; San Juan Mountains, Colorado; Sierra Nevada, California; and Jasper National Park, Alberta (Major and Taylor 1977, Hrapko and La Roi 1978, Komarkova 1979, Hartman and Rottman 1985). It is absent from the Beartooth Plateau, Montana, but has been documented from other mountain ranges in Montana (Johnson and Billings 1962, Bamberg and Major 1968).

CONCLUSIONS

East central Idaho supports a considerable array of alpine plant communities that we are just beginning to discern. This study focused on a single alpine area and described 8 distinctive communities based on habitat specificity. Environmental factors such as substrate and elevation were highly correlated with observed community variation, but moisture status and slope were also important in describing distribution and occurrence of these communities. Some communities, such as those dominated by *Salix nivalis* and *Artemisia campestris*, were restricted to 1 substrate type and showed narrow habitat ranges. At the opposite extreme, *Geum rossii* communities spanned a wide range of environmental conditions.

The 8 community types described here represent some of the general physiognomies found in other North American alpine areas (e.g., turf, fellfield, and snowbed). Sedge-dominated communities and *Geum rossii* communities similar to those found at Railroad Ridge have been documented throughout North America's temperate alpine habitats. Open, dry fellfields dominated by *Phlox pulvinata* are commonly found on upper windward slopes in the mountain ranges of east central Idaho and some ranges in the Great Basin. Other communities, such as *Ivesia gordonii*–dominated fellfields, are uncommon and known from only a few alpine sites in Idaho and the Great Basin.

Earlier studies of the Idaho alpine zone have all documented community types not previously known to exist within the state. This study was no exception; *Artemisia campestris* is unique not only because it dominates communities on Railroad Ridge, but also because it is not known from other alpine areas in the state. Also, *Eriogonum ovalifolium* and *Silene acaulis* have not been described in an association like that found on Railroad Ridge. Future studies are likely to continue documenting undescribed communities in east central Idaho.

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APPENDIX. List of plant species used in TWINSPAN and CCA analyses and associated abbreviations displayed in TWINSPAN dendrogram (Fig. 3) and in CCA ordination diagrams (Figs. 4, 5).

Species	Abbreviations
Agoseris glauca (Pursh) Raf. var. *glauca*	Ag
Androsace septentrionalis L.	As
Antennaria umbrinella Rydb.	Au
Arenaria congesta Nutt. var. *cephaloidea* (Rydb.) Maguire	Ac
Arenaria obtusiloba (Rydb.) Fern.	Ao
Artemisia campestris L. ssp. *borealis* (Pall.) Hall & Clem. var. *purshii* (Bess.) Cronq.	Aca
Aster alpigenus (T. & G.) Gray	Aa
Astragalus kentrophyta Gray var. *implexus* (Canby) Barneby	Ak
Bupleurum americanum Coult. & Rose	Ba
Carex elynoides T.H. Holm	Ce
Carex phaeocephala Piper	Cp
Draba densifolia Nutt.	Dd
Elymus elynoides (Raf.) Swezeyn	Ee
Erigeron compositus Pursh var. *glabratus* Macoun	Ec
Erigeron simplex Greene	Es
Eriogonum flavum Nutt. var. *piperi* (Greene) Jones	Ef
Eriogonum ovalifolium Nutt. var. *depressum* Blank.	Eo
Eritrichium nanum (Vill.) Schrad. var. *elongatum* (Rydb.) Cronq.	En
Festuca ovina L. var. *brevifolia* (R. Br.) Wats.	Fb
Festuca ovina L. var. *ingrata* Hackel ex Beal	Fi
Geum rossii (R. Br.) Ser. var. *turbinatum* (Rydb.) Hitchc.	Gr

APPENDIX. Continued.

Species	Abbreviations
Haplopappus lanuginosus Gray var. *lanuginosus*	Hl
Hymenoxys grandiflora (T. & G.) Parker	Hg
Ivesia gordonii (Hook.) T. & G.	Ig
Lomatium foeniculaceum (Nutt.) Coult. & Rose var. *macdougalii* (Coult. & Rose) Cronq.	Lf
Lupinus argenteus Pursh var. *depressus* (Rydb.) Hitchc.	La
Luzula spicata (L.) DC.	Ls
Oxytropis campestris (L.) DC. var. *cusickii* (Greenm.) Barneby	Oc
Oxytropis viscida Nutt.	Ov
Penstemon procerus Dougl. ex. R. Grah. var. *procerus*	Pp
Phlox pulvinata (Wherry) Cronq.	Ppu
Poa fendleriana (Steudel) Vasey	Pf
Poa glauca Vahl var. *rupicola* (Nash) J. Boivin	Pg
Poa secunda Presl	Ps
Potentilla diversifolia (Lehm.) var. *diversifolia*	Pd
Potentilla ovina Macoun.	Po
Salix nivalis Hook. var. *nivalis*	Sn
Sedum lanceolatum Torr. var. *lanceolatum*	Sl
Selaginella densa Rydb.	Sd
Silene acaulis L.	Sa
Silene repens Pers.	Sr
Smelowskia calycina (Steph.) C.A. Mey.	Sc
Trisetum spicatum (L.) Richter	Ts

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THROUGHFALL VOLUME AND CHEMISTRY AS AFFECTED BY PRECIPITATION VOLUME, SAPLING SIZE, AND DEFOLIATION INTENSITY

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ABSTRACT.—Throughfall and stemflow are important components of hydrologic processes in forests, but relative contributions of multiple factors, including precipitation volume, plant size, and folivory (leaf removal by defoliators), on throughfall/stemflow have not been reported. This paper reports the relative influences of precipitation volume (0–230 L m^{-2}), sapling size (1.4–6.7 cm diameter at root collar; 0.07–0.45 kg calculated dry foliage mass), and manipulated folivory (0–20% foliage removal) on throughfall volume and N, K, and Ca fluxes as evaluated with stepwise multiple regression in a young Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) ecosystem.

Precipitation volume explained most variation in throughfall volume ($R^2 = 0.81$). Folivory and sapling size each had significant but minor effects on throughfall volume and nutrient fluxes. These data indicate that folivore effects, while significant, are masked by precipitation in this wet ecosystem. Wider ranges in sapling size and folivory and/or drier conditions likely would improve interpretation of their influence on throughfall volume and chemistry.

Key words: throughfall, nutrient cycling, defoliation, nitrogen, potassium, calcium, conifer, ecosystem, forest, plantation.

Forest canopies are the major interface between the biosphere and atmosphere, filtering water, nutrients, and aerosols and determining the rate of ecosystem acquisition of these resources. The canopy also modifies the chemistry of precipitation percolating through it and reaching the forest floor as throughfall and stemflow (hereafter, throughfall). Water intercepted by the canopy affects canopy processes (such as evapotranspiration) and soil/litter processes (such as erosion, leaching, and decomposition). Hence, factors influencing volume and chemistry of throughfall are key regulators of hydrologic and biogeochemical cycling processes.

Several factors contribute to throughfall volume and chemistry, especially precipitation volume and chemistry, canopy surface area, and folivory, or leaf area removed by defoliators (Parker 1983, 1995, Lovett et al. 1996). Precipitation volume clearly affects the amount of water that penetrates the canopy and contributes to leaching from foliage surfaces. Low precipitation volumes may be entirely intercepted by the canopy, whereas volumes exceeding canopy storage capacity contribute to throughfall (Rothacker 1963, Rutter et al. 1975, Gash 1979). Interception by the canopy depends on canopy surface area, which increases as trees grow (Parker 1983). Hence, throughfall volume is inversely proportional to canopy surface area. Folivory (consumption of foliage) reduces foliage surface area and increases the rate at which water and nutrients (via leaching from damaged leaves and litterfall components) reach the forest floor (Kimmins 1972, Seastedt et al. 1983, Schowalter et al. 1991).

Previously, the effects of factors influencing throughfall have been studied separately, so their relative contributions in a single study are unknown. Few studies have evaluated folivore effects experimentally. Schowalter et al. (1991) reported that throughfall volume and nutrient turnover were significantly correlated with manipulated folivore abundance on young Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in western Oregon, but only during the relatively dry spring and summer. Regression coefficients for effects of folivore abundance were low, further indicating important effects of other varying factors in that study, such as precipitation and sapling size. Measurements of precipitation volume and sapling size, as well as folivore abundance, in that study provide a unique opportunity to evaluate the degree to which precipitation volume and sapling size influenced folivore effects on throughfall.

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MATERIALS AND METHODS

This study was conducted on watershed 10 at the H.J. Andrews Experimental Forest Long Term Ecological Research (LTER) site from April 1984 to April 1986. The Andrews Forest is a 6100-ha facility in the central western Cascades of Oregon (latitude 44°N, longitude 122°W) operated jointly by the USDA Forest Service Willamette National Forest and Pacific Northwest Research Station and Oregon State University. Elevation ranges from 500 to 1500 m. The maritime climate is characterized by wet, relatively mild winters and dry, warm summers. Average annual temperature is 7.9°C; average annual precipitation is 2400 mm, with >75% occurring as rain from October through April. Snow is frequent, but accumulations are rare and of short (<2 wk) duration at the study site (Grier and Logan 1977, Gholtz et al. 1985).

Watershed 10 covers 10 ha at the western boundary of the Andrews Forest. Elevation is 430–670 m with slopes of 25–50%. This site was harvested and replanted with Douglas-fir during 1975 (Gholtz et al. 1985). At the initiation of this study, 1- to 1.5-m-tall Douglas-fir saplings were widely spaced (2–4 m apart) and intermixed with young maple (*Acer* spp.) and dogwood (*Cornus*) sprouts, as well as various shrubs and herbs. Foliage loss to herbivores in young Douglas-fir on this and other sites at the Andrews Forest typically is <1% of standing crop, but has ranged up to 10% (Schowalter 1989, 1995, and unpublished data).

Thirty Douglas-fir within a 1-ha area on the north-facing slope were involved in this study. These saplings were selected on the basis of similarity in crown geometry, foliage color, and density; absence of prior deer browsing; and relative isolation from surrounding vegetation. Selections attempted to minimize variation that could confound isolation of factors affecting throughfall chemistry (Schowalter et al. 1991). All naturally occurring herbivores were manually removed every 2 wk. Ten trees served as an herbivore-free treatment. The remaining trees were treated to an experimental range of intensities (5–60 caterpillars kg foliage^{-1}) of the silver-spotted tiger moth, *Lophocampa argentata* (Packard) (Lepidoptera: Arctiidae), a common, naturally occurring folivore found at elevated population levels in the Cascades during the experimental period. This range of intensities caused 0–20% foliage removal, compared to typical rates of 0–10% in this forest (e.g., Schowalter 1995). Caterpillar density was manipulated by counting and replacing missing caterpillars every 2 wk to maintain target densities (Schowalter et al. 1991). Foliage mass was calculated from measured stem diameter, as described below.

Experimental saplings could not be killed for direct measurement of mass. Stem diameters were measured at the root collar in April (before new foliage production and new stem growth) each year. Because foliage mass should be a better predictor than sapling diameter of sapling capacity to intercept precipitation (thereby affecting throughfall), dry foliage mass was estimated for each tree as

$$\ln Y_F = 3.8 + 1.3 \ln X \ (P < 0.0001, R^2 = 0.91),$$

where X is stem diameter in centimeters (range 0.3–6.1 cm), and Y is dry foliage mass in grams (M. Klopsch unpublished LTER data, 1989).

The regular conical crown oriented along the bole axis for young conifers simplified collection of throughfall and stemflow for each sapling. Triangular, galvanized steel pans, 8 cm deep with a 36° angle fitted to the bole (to collect stemflow with throughfall) and covered beyond the crown perimeter (to avoid nonintercepted precipitation), were used to collect throughfall, stemflow, and litterfall from 10% of the area covered by the crown. Covers were reduced as crown diameters increased. Hence, sampled area ranged from 0.04 m^2 to 0.08 m^2. Collectors were connected by plastic tubing to a 20-L plastic bottle that stored throughfall. An aluminum mesh (1 × 1 mm) was inserted into each collector to retain particulate material and prevent blockage of the drain. Although litterfall was removed from the collectors every 2 wk, throughfall likely was augmented to some extent by nutrients leached from litterfall intercepted by the mesh. An additional 3 collectors (identical construction) were placed in open areas to sample incident precipitation.

Precipitation and throughfall were measured in L m^{-2} interception area. A 1-L subsample was collected every 2 wk during the wet season (November–April) and after individual rainfall events during the remainder of the year. Forty-five collections were made over the 3-yr period. Subsamples were filtered and frozen until they could be thawed and analyzed for elemental concentrations, using autoanalyzer techniques for Kjeldahl N and standard atomic absorption spectrophotometry for K and Ca. These elements were selected for analysis because of their biological importance (N in protein and nucleic acids, K and Ca for muscle and nerve activity), their relevance to previous studies of folivore effects (e.g., Kimmins 1972, Seastedt et al. 1983, Schowalter et al. 1991), and the range of ecological mobilities represented (K highly mobile, Ca relatively immobile; e.g., Gholtz et al. 1985). Biweekly sampling was appropriate because precipitation is nearly continuous between November and April, low temperatures during this period limit microbial activity, microbicides could confound elemental analyses, and earlier studies indicated satisfactory results of this timing for N (Klingaman and Nelson 1976). The collection bottles were washed in 1 N H_2SO_4 and rinsed with deionized water every 6 mon.

Sapling diameter and calculated foliage mass were divided by 10 to represent the 10% area sampled. Nutrient concentrations in throughfall were multiplied by throughfall volumes for each sample to calculate g m^{-2} in throughfall. Nutrient concentrations in precipitation were multiplied by precipitation volume to calculate g m^{-2} which were then subtracted from throughfall to indicate net nutrient fluxes.

Data were transformed, as necessary, using natural logarithms to improve normality and homoscedasticity. Stepwise multiple regression was used to evaluate relative contributions of precipitation volume, sapling size (diameter or foliage biomass), and folivore intensity on throughfall volume and net N, K, and Ca fluxes. Because diameter and foliage biomass were correlated variables, separate analyses were used for these variables. Variables were required to meet a $P < 0.15$ significance level to be added to the regression equation, but were considered significant only if $P < 0.05$. Each regression had 1000–1345 (30 saplings × 45 collections) error degrees of freedom, depending on numbers of missing values. SAS software (SAS Institute 1982) was used for statistical analyses.

RESULTS

Precipitation volumes for individual collections ranged from 0 to 230 L m^{-2} (0–230 mm of precipitation). Sapling sizes ranged from 1.4–4.8 cm diameters the 1st yr to 2.3–6.7 cm diameters the 3rd yr. Calculated foliage mass ranged from 0.07–0.35 kg the 1st yr to 0.15–0.45 kg the 3rd yr. Manipulated folivore intensity (number kg $foliage^{-1}$) ranged from 0 to 0.06 g^{-1} foliage, resulting in 0–20% foliage reduction, estimated visually.

Results for regressions incorporating these variables are shown in Table 1. Several results are noteworthy. First, precipitation clearly had a dominant effect on throughfall. Plant size and folivory had significant, but relatively unimportant, effects ($R^2 < 0.2$). Second, although foliage mass was calculated as a function of stem diameter, the regression equations resulting from the 2 measures of plant size differ, especially in the sign of the plant size effect (+ for diameter, – for foliage mass) on flux of all 3 elements. Third, the folivore effect was significant only for K flux when stem diameter was included, but the slope was negative using either measure of plant size.

DISCUSSION

Although Schowalter et al. (1991) reported that folivory significantly affected seasonal throughfall and net nutrient fluxes when standardized for sapling size, this study (using the same dataset) indicated that precipitation and sapling size had greater effects on throughfall volume and chemistry than did manipulated folivore abundance. The long, narrow structure of conifer needles and the typical truncation of needles by conifer defoliators probably minimize the surface area available for leaching following wounding, perhaps minimizing the folivore effect on leaching losses, especially of K, which is highly leachable from foliage. However, needle loss should reduce canopy interception capacity and hence increase throughfall volume.

Precipitation volume was the most important predictor of throughfall volume, and the wide range of precipitation volumes likely masked the influence of the other 2 factors, which had relatively narrow ranges. Sapling size and folivory each had significant (but minor) effects on throughfall volume, with volume showing the expected decrease with sapling size and increase with folivore intensity.

Effects of sapling size and folivory on fluxes of N, K, and Ca were less clear. Sapling diameter was a better predictor of throughfall volume and chemistry (higher P and R^2),

TABLE 1. Parameter estimates (± standard errors), F statistics, and partial correlation coefficients for regression equations to predict throughfall volume and N, K, and Ca fluxes from precipitation volume, sapling size (stem diameter in cm or foliage mass in kg), and herbivore intensity in regenerating Douglas-fir in western Oregon.

Y[a]	X_i[b]	Parameter estimate	Standard error	F	*P*	Partial R^2
Volume	Intercept	16	3.6	21	0.0001	
	Precipitation	1.0	0.01	5600	0.0000	0.81
	Diameter	–7.9	0.95	70	0.0001	0.010
	Folivore intensity	13	4.7	7	0.008	0.001
Volume	Intercept	–5.1	3.1	3	0.1	
	Precipitation	1.0	0.0	5600	0.0000	0.81
	Folivore intensity	13	4.8	7	0.007	0.001
	Foliage mass	–0.01	–0.01	4	0.059	0.0005
N	Intercept	95	35	8	0.006	
	Diameter	89	8.6	100	0.0001	0.09
	Precipitation	0.3	0.1	6	0.02	0.005
N	Intercept	510	28	330	0.0001	
	Foliage mass	–0.3	0.1	14	0.0002	0.01
K	Intercept	–550	180	9	0.002	
	Diameter	650	44	210	0.0001	0.17
	Folivore intensity	–450	220	5	0.03	0.004
	Precipitation	1.3	0.67	4	0.05	0.003
K	Intercept	2000	160	160	0.0001	
	Foliage mass	–0.8	0.4	5	0.03	0.004
	Folivore intensity	–387	247	3	0.117	0.003
Ca	Intercept	–85	90	1	0.34	
	Precipitation	3.7	0.3	120	0.0001	0.09
	Diameter	160	22	49	0.0001	0.04
Ca	Intercept	730	76	93	0.0001	
	Precipitation	3.5	0.3	110	0.0001	0.09
	Foliage mass	–0.8	0.2	19	0.0001	0.02

[a] Volume in L m^{-2} 2-wk $period^{-1}$; N, K, and Ca in g m^{-2} 2-wk $period^{-1}$

[b] Precipitation in L m^{-2}, tree diameter in cm, foliage mass in kg, and herbivore intensity in number kg $foliage^{-1}$

compared to calculated foliage mass (which should better represent the surface area for interception and nutrient flux). Fluxes of K and Ca should be proportional to foliage mass or area because of net leaching from foliage, especially for K, whereas N flux should reflect canopy uptake (Lovett et al. 1996). Fluxes of all 3 elements were positively correlated to sapling diameter, but negatively correlated to foliage mass. Because these 2 measures of plant size were highly correlated, their different effects on regression analysis suggest that the range of values was too small, compared to other factors, or that interaction with other factors influenced their effects.

Nutrient fluxes, especially of K, have been positively related to folivore intensity in earlier studies (Kimmins 1972, Seastedt et al. 1983, Schowalter et al. 1991). When effects of folivory were standardized by foliage mass, N, K, and Ca fluxes were significantly positively related to folivore intensity (Schowalter et al. 1991). However, when effects of folivory were standardized by ground area in this study, K flux was negatively related to folivore intensity and fluxes of other nutrients were not significant (Table 1). These results suggest that different methods used to standardize data influenced the apparent effect of folivores, perhaps because standardized area exacerbated deviation of calculated foliage mass from actual foliage mass as reduced by folivory. These differences should be noted by ecologists who measure and standardize throughfall based on ground area or plant size.

The range of sapling sizes (1.4–6.0 cm diameter) and folivory (0–0.06 caterpillars kg $foliage^{-1}$, causing 0–20% foliage reduction) was relatively narrow compared to the range of precipitation volumes in this study. The wide range of precipitation volumes dominated regression analyses and probably masked the effects of narrower ranges in other factors and may even have influenced their apparent relationships to throughfall chemistry. Studies relating throughfall volume and chemistry to a wider range of plant size and/or folivory should improve the predictive power of models reported here. Alternatively, better separation of litter and throughfall nutrients under drier conditions could improve resolution of nutrient fluxes.

Regression equations can be used to calculate the effect of each factor on throughfall volume. A 2-cm-diameter sapling would intercept virtually no precipitation, regardless of volume, whereas a 6-cm-diameter sapling could intercept about 32 L m^{-2} before throughfall appeared. At the maximum precipitation volume observed in this study (230 L m^{-2}), a 6-cm-diameter sapling would intercept about 14%, within the range of 10–30% for various older forests, as reviewed by Parker (1983). Rothacker (1963) reported interception ranging from 100% for storms less than 10 L m^{-2} (0.05 inch) to 18% for storms over 75 L m^{-2} (3 inches) and estimated interception at only 4% for storms over 180 L m^{-2} (7 inches) in old-growth Douglas-fir stands at the Andrews Forest.

The larger calculated proportion of precipitation intercepted in this study, compared to Rothacker's, likely reflects my integration of several precipitation events, generally over 2-wk periods (compared to individual storm volumes in Rothacker's study), and my selective placement of throughfall collectors under crowns (compared to random placement in Rothacker's study). Selective placement of throughfall collectors under crowns limits comparison between these data and those from collectors placed randomly. However, more controlled conditions for throughfall collection in this study better represent the linkage between canopy processes and throughfall. Nonetheless, potential influences of these 2 collection methods on evaluation of folivore, or other, effects should be noted. Data for individual trees and open areas can be integrated to model throughfall under a heterogeneous canopy, but data collected without reference to canopy structure cannot be extrapolated.

In conclusion, this study is the first to evaluate relative effects of precipitation volume, sapling size, and folivory on throughfall volume and chemistry. These data indicate that precipitation volume in this temperate rainforest had the greatest effect on throughfall volume. Although sapling size and folivore abundance significantly affected throughfall volume and N, K, and Ca fluxes, their effects were largely masked (and perhaps modified) by precipitation volume when analyzed by multiple regression in this study. Folivore effects should be more important under drier conditions that typically promote folivore outbreaks.

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FACTORS ASSOCIATED WITH WETWOOD INTENSITY OF *POPULUS FREMONTII* (FREMONT COTTONWOOD) IN ARIZONA

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ABSTRACT.—Wetwood is a condition of *Populus fremontii* and other tree species characterized by staining and water soaking in the heartwood, bleeding from wounds and stem junctions, and leaf and branch dieback. A field survey indicated that wetwood symptoms were present in populations of *Populus fremontii* at all 17 riparian sites surveyed in Arizona. However, incidence and severity of bleeding symptoms varied within and among sites. Within sites, incidence and severity increased with tree size. In the smallest size class of trees (1–32 cm dbh), incidence (% of trees with wetwood bleeding symptoms) ranged among sites from 14% to 83%, and mean severity ranged from 1.1 to 2.6 (on a 5-point scale). Closer host spacing (i.e., greater density), more homogeneous stand composition, finer substrate texture, and channel instability all were significantly correlated with increased expression of wetwood symptoms. Bleeding symptoms also were significantly correlated with canopy effects. As the severity of bleeding symptoms increased, so did canopy decline independent of changes in host density.

Key words: wetwood, Populus fremontii, *disease severity, riparian habitat, bacteria, canopy decline.*

Wetwood occurs in the heartwood of *Populus fremontii* Wats (Fremont cottonwood) and other tree species and is characterized by dark brown staining and infusion of water (Ward and Pong 1980, Murdoch and Campana 1981). High internal pressures develop in trees with internal wetwood symptoms resulting in the bleeding or "fluxing" of liquid from wounds and stem junctions. When contaminated with bacteria, yeasts, and other fungi, the liquid forms a fetid, foaming mass known as slime flux. Profuse bleeding can cause liquid to flow down bark, forming a light gray or white incrustation on the bark when dried. Branch dieback may occur, and the entire crown can decline over several years.

Several aerobic bacteria (Carter 1945, Teidemann et al. 1977, Murdoch and Campana 1983) or anaerobic bacteria (Shigo et al. 1971, Zeikus and Ward 1974, Zeikus and Henning 1975, Teidemann et al. 1977, Schink et al. 1981) have been associated with wood in trees with wetwood symptoms, but the pathogenicity of these bacterial isolates has not been proven. Some investigators have suggested that causes of wetwood are physiological and result in changes in wood that promote bacterial growth (Knutson 1973, Bauch et al. 1975, Teidemann et al. 1977, Ward and Pong 1980). Bacteria are directly involved in the production of external symptoms associated with internal wetwood symptoms (Rasmussen-Dykes and Jacobi 1995)

Regardless of causative factors, biotic and abiotic environmental conditions are known to influence the development of wetwood in tree species. Wetwood symptoms have been shown to increase with host age, but symptoms do occur in very young trees (Hartley et al. 1961, Ward and Pong 1980). In some cases moist or swampy sites are associated with high incidences of wetwood (Ward and Pong 1980). External wetwood symptoms have been associated with insect attacks (Hartley et al. 1961), stem cankers of dwarf mistletoe (Wilcox et al. 1973), and physical wounding including broken branches, pruning cuts, and systemic pesticide injection holes (Murdoch and Campana 1980, Ward and Pong 1980). Wetwood symptoms are prevalent in many ornamental shade trees including elm, cottonwood, aspen, and willow (Horne 1983, Rasmussen-Dykes and Jacobi 1995). In landscapes stress conditions including drought increase problems associated with wetwood (Rasmussen-Dykes and Jacobi 1995).

Populations of *P. fremontii*, a dominant tree species in riparian ecosystems of the U.S. Southwest, were observed with bleeding or fluxing symptoms and canopy dieback. Bleeding was observed from all woody plant parts including roots and the entire length of stems. Sources of bleeding included branch junctions, ends of broken limbs, insect bore holes, frost ribs, and other wounds of undetermined nature. Examination of cores from trunks of trees with these external symptoms revealed darkly discolored, water-soaked wood. The objectives of this investigation were to ascertain the extent of wetwood symptoms in *P. fremontii* populations in Arizona and to determine some host and environmental factors associated with high incidences and severity of wetwood symptoms.

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MATERIALS AND METHODS

Wetwood Symptoms

We quantified severity and incidence of wetwood symptoms and extent of canopy dieback for *P. fremontii* at 17 riparian sites in Arizona (Fig. 1). Sites were chosen to encompass a range of environmental conditions in which *P. fremontii* occur. At sites with narrow riparian corridors, we randomly selected 50 *P. fremontii* trees. At sites with wide flood plains, the 50 trees were selected in stratified random fashion by dividing the flood plain into lateral strips of varying distances from the active channel. This insured the sampling of trees in the range of size classes present.

We used a 5-point scale (Table 1) to quantify severity of wetwood symptoms for each tree. Severity was assessed based on quantity and size of bleeding sources (including branch junctions, branch stubs, cracks, and other wounds) per tree. Bleeding sources were divided into minor and major sources based on size, flow rate, and presence of bark incrustation. The severity scale had greatest sensitivity at the low end of the scale and lost sensitivity at the top end in that all trees receiving a rank of 5 did not have equivalent amounts of wetwood symptoms. We defined incidence in a binary fashion based on presence or absence of wetwood symptoms. All trees scoring a rank of 1 on the severity scale were considered to be free of wetwood symptoms. Incidence was calculated as the percentage of trees with symptoms relative to the total sample of trees. These methods may underestimate incidence because not all individuals that show internal wetwood symptoms also express bleeding symptoms (Toole 1968). The percent of maximum canopy (PMC) present was estimated for each tree, taking into consideration the presence of broken, missing, or otherwise damaged limbs and trunks, branch dieback, and wilting. Maximum canopy was defined as the maximum canopy development that would occur under ideal growing conditions.

Host and Environmental Conditions

We measured each *P. fremontii* tree for trunk diameter at 1.5 m above ground level (dbh), distance (m) from the trunk to the edge of the nearest channel, and distance to the nearest adjacent *P. fremontii.* Because willows (*Salix* spp.) were observed also to have wetwood symptoms, we recorded distance to the nearest willow tree. Elevation (m) above the channel thalweg was estimated for each tree. Height of flooding debris was recorded as an indication of magnitude of the most recent flood (statewide flooding occurred in winter 1995). Each tree was inspected for the presence of wounds, mistletoe, tent caterpillars, and bark beetle damage.

For each site we visually characterized tree species composition as *P. fremontii* dominated, *P. fremontii–Salix* dominated, or "mixed" (vegetated by a mixture of *P. fremontii*, *Salix* sp., *Juniperus* sp., *Quercus* sp., *Platanus wrightii*, *Fraxinus* sp., and/or *Alnus* sp.). Surface flow frequency was characterized as either ephemeral or perennial, based on literature review, conversations with site managers, or review of USGS stream gage data. Channel morphology was described as either multichanneled (i.e., braided) or confined to a well-defined single channel; this variable was designated as channel stability. Predominant substrate particle size was visually classified as silt, sand, gravel, or cobbles. Information on site elevation (as a surrogate for site temperature) and stream gradient was obtained from topographical maps.

Statistical Analysis

Within sites, Pearson correlation analysis was used to examine the relationship of wetwood severity with tree size, distance to the stream channel and above the thalweg, and distance to nearest neighbors. Correlation analysis also was used to assess the relationship between individual severity of wetwood bleeding symptoms and dbh, using data pooled across sites.

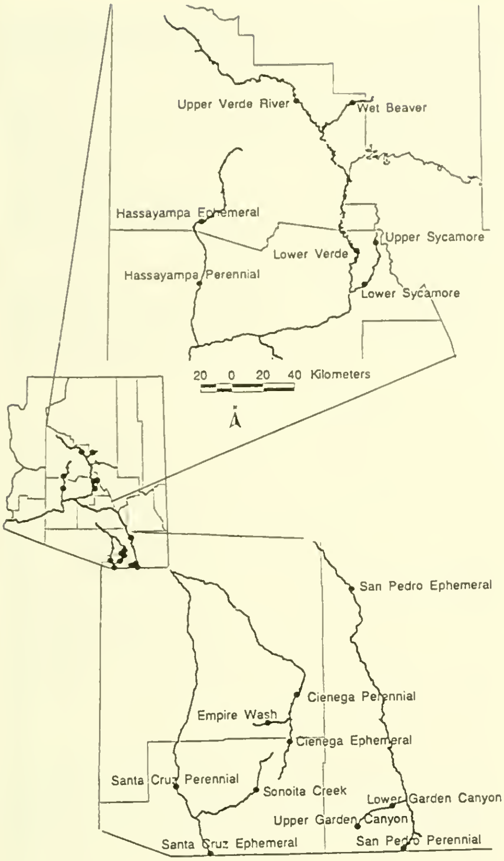

Fig. 1. Locations of the 17 study sites found in riparian areas in Arizona where wetwood incidence and severity were assessed.

To facilitate among-site analysis, we assigned trees to 1 of 6 size (dbh) classes (1–32 cm, 33–64 cm, 65–96 cm, 97–128 cm, 129–160 cm, 161–192 cm). Incidence and mean severity were compiled by size class for each site. Relationships between incidence and mean severity values for size classes 1 and 2 (the only size classes present at all 17 sites) and mean site values for host and environmental conditions (using a mix of cardinal and ordinal variables) were analyzed with Pearson correlation analysis and forward stepwise multiple regression analysis (SPSS). Correlation analysis also was used to examine interrelationships of site variables. Average site value for percent maximum canopy (PMC) was correlated with site averages for incidence and severity of wetwood symptoms and other site and host variables.

RESULTS

We observed wetwood bleeding symptoms on *P. fremontii* at all 17 sampling sites. Incidence and mean severity of wetwood bleeding symptoms varied substantially within and among sites. Within sites, incidence and severity varied strongly with tree size. Incidence and mean severity increased from the smallest size class to the largest size class present (Table 2, Fig. 2), and individual severity of wetwood bleeding symptoms was significantly correlated with individual dbh ($P < 0.01$, $r = 0.55$, $n = 850$, data pooled across sites). Distance to channel and elevation above channel for each tree were also significantly correlated with severity at several sites; however, distance and elevation relative to channel were also significantly correlated with host dbh at $P < 0.05$.

For size class 1, incidence ranged among sites from 14% at Wet Beaver Creek to 80% at Empire Wash, and mean severity ranged from 1.1 at Wet Beaver Creek to 2.6 at the Santa Cruz Ephemeral site (Table 2). For size class 2, values for incidence ranged among sites from 43% to 87%, and mean severity ranged from 1.9 to 4.5. *Populus fremontii* spacing, stand composition, substrate texture, and channel stability were all significantly correlated (at $P < 0.05$) with incidence or severity of size class 1 or 2 (Fig. 3, Table 3). Stream flow frequency and bark beetle incidence were, respectively, negatively and positively correlated with wetwood incidence (at $P < 0.10$; Table 3). However, substrate texture and density-related variables (mean *P. fremontii* spacing, stand composition) were the only variables included in the multiple regression models (Table 4). Substrate texture was strongly correlated with several other site variables, including channel stability ($P < 0.01$, $r = 0.73$), stream gradient ($P < 0.01$, $r = 0.56$), stand composition ($P < 0.05$, $r = 0.50$), and site elevation ($P < 0.08$, $r = 0.44$). *Populus fremontii* spacing was significantly correlated among sites only with mean *P. fremontii* dbh ($P < 0.01$, $r = 0.65$; i.e., correlation between larger trees and lower density).

Site factors not significantly correlated with incidence and severity included site elevation, height of flooding, stream gradient, mean distance to nearest willow, physical wounding (primarily flood damage), and incidences of mistletoe and tent caterpillars. The incidences

TABLE 1. Severity scale and definitions used to quantify bleeding symptoms of wetwood.

Bleeding symptoms observed	Severity class
No bleeding sources	1
One minor bleeding source	2
Two minor bleeding sources, or one major bleeding source	3
Three to four minor bleeding sources, or two to three major bleeding sources	4
More than four minor bleeding sources, or more than three major bleeding sources	5

of mistletoe, tent caterpillar, and bark beetle damage were highly variable between sites. These organisms were not detected in trees at most sampling sites, but they occurred at higher incidences (>30%) at a few sites. For example, bark beetle infestation was detected at these levels at only 2 sites (Santa Cruz Ephemeral and Perennial).

Mean site value for the percentage of maximum canopy (PMC) was significantly correlated ($P < 0.01$, $r = -0.62$, $n = 17$) with mean site severity. As severity of bleeding symptoms increased, so did canopy decline. Natural pruning is common, especially in the lower canopy of dense stands; however, there was no significant correlation between PMC and stand density ($P > 0.10$, $r = 0.23$). Percent optimal canopy decreased significantly with increasing site elevation, but not with other measured factors.

DISCUSSION

We found wetwood symptoms to be widespread in *P. fremontii* populations at riparian ecosystems in Arizona. It is likely that values for wetwood incidence were greater than this investigation reports because incidence calculations were based on external symptoms only. Toole (1968) reported that liquid flowed from core wounds in only 30% of affected cottonwood trees. In addition, Murdoch and Campana (1981) report that elm trees in the western U.S. show more variability in internal disease development and significantly less bleeding and symptom expression than those in the eastern U.S.

Certain host and site characteristics found to be associated with higher incidences and severity of wetwood symptoms have been reported by others as well. As *P. fremontii* increased in size (and age; Hinchman and Birkeland 1995), severity and incidence of wetwood symptoms increased. Toole (1968) and Murdoch and Campana (1981) similarly found that wetwood intensity increased with tree age in eastern cottonwood and elm, although Etheridge and Morin (1962) reported wetwood to be more prevalent in younger balsam fir. Many foresters agree that wetwood is associated with older trees (Ward and Pong 1980), but they also report that *Populus* is susceptible to wetwood at all ages.

As substrate particle size decreased, incidence and severity of wetwood symptoms in *P. fremontii* increased. This relationship may be a consequence of increased water-holding capacity and decreased aeration that occur at finer soil textures and is thus consistent with observations of high incidences of wetwood for some tree species at moist or swampy sites (Ward and Pong 1980). However, wetwood expression increased as surface flow frequency decreased, as evidenced by negative correlations between surface flow frequency and severity of bleeding for class 1 trees. More investigation is needed regarding wetwood symptom expression in Fremont cottonwood in relation to soil moisture.

Similar to other studies (Hartley et al. 1961, Bauch et al. 1975), we found some correlation between wounding (i.e., bark beetle damage) and the occurrence of wetwood symptoms. Lack of significant relationships for other types of wounding may have resulted from the highly variable nature of wounds between sites, as well as from an inability to detect and accurately quantify wounding. For example, flood-related wounds located near the root crown could be buried at some sites under a meter or more of sediment (Stromberg et al. 1991).

Relationship between density-related variables (mean tree spacing, stand composition) and wetwood incidence and severity has received little research attention. High stand densities may affect wetwood incidence and severity by increasing competition for nutrients and water and affecting growth rates of individual cottonwood trees. Density also affects the microenvironment of a stand, leading to changes in light intensity, temperatures, and relative humidity, all of which may affect wetwood incidence and severity. An intriguing

TABLE 2. Incidence and mean severity of wetwood symptoms on *Populus fremontii* by size (dbh) class for 17 riparian sites in 4 Arizona watersheds.

	Incidence (%)						Severity					
Site	1[a]	2	3	4	5	6	1	2	3	4	5	6
VERDE RIVER BASIN												
Wet Beaver	14	43	50				1.2	1.9	1.7			
Lower Sycamore	26	53	100				1.4	1.9	3.0			
Upper Sycamore	29	69					1.4	1.9				
Lower Verde	64	86					1.9	2.6				
Upper Verde	48	94	60	100			1.9	3.3	3.2	5.0		
MIDDLE GILA RIVER BASIN												
Hassayampa Perennial	35	96	100				1.5	3.2	3.0			
Hassayampa Ephemeral	77	100					2.3	4.0				
SANTA CRUZ RIVER BASIN												
Santa Cruz Perennial	35	75					1.5	2.8				
Sonoita Creek	30	100	100	100			1.4	3.5	4.2	5.0		
Cienega Perennial	76	100	100				2.2	2.8	2.0			
Empire Wash	80	80	100	100			2.5	2.8	5.0	5.0		
Santa Cruz Ephemeral	76	100	100	100	100		2.6	3.7	5.0	5.0	5.0	
Cienega Ephemeral	55	100	100	100	100	100	2.1	4.5	4.5	5.0	5.0	5.0
SAN PEDRO RIVER BASIN												
Upper Garden Canyon	41	83	75				1.5	2.3	2.3			
Lower Garden Canyon	33	100	100				1.4	2.7	3.0			
San Pedro Perennial	66	100					2.1	3.3				
San Pedro Ephemeral	83	100					2.2	2.5				

[a] Size class 1 = 1–32 cm dbh, class 2 = 33–64 cm, class 3 = 65–96 cm, class 4 = 97–128 cm, class 5 = 129–160 cm, class 6 = 161–192 cm

question is whether the very high incidence of wetwood at some study sites reflects unnaturally high stand densities for *P. fremontii.* Irruptions of tree populations—and associated irruptions of disease or insect outbreaks—can be an indicator of reduced ecosystem integrity (Costanza et al. 1992). Such irruptions can result from human management practices that diverge from evolutionary history of a population or ecosystem (Covington and Moore 1994). Presently, conditions along some rivers in this study contrast with historical descriptions. For example, historical descriptions of the San Pedro refer to a mosaic of forest and marshland rather than to corridors of high-density forest stands. Changes in tree density may be a response to local extirpation of beaver, an agent of geomorphic and biological change that historically served to create a more patchy, heterogeneous flood plain community.

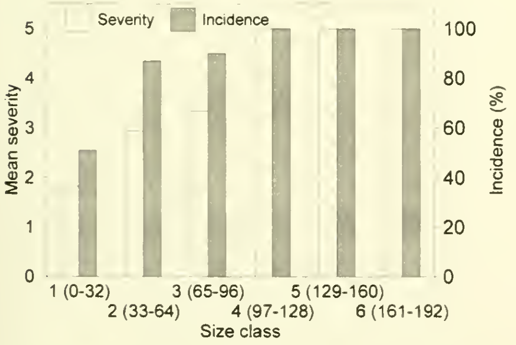

Fig. 2. Mean severity and incidence of wetwood bleeding symptoms observed for 6 stem diameter (cm) size classes of *Populus fremontii* for all sites sampled in Arizona.

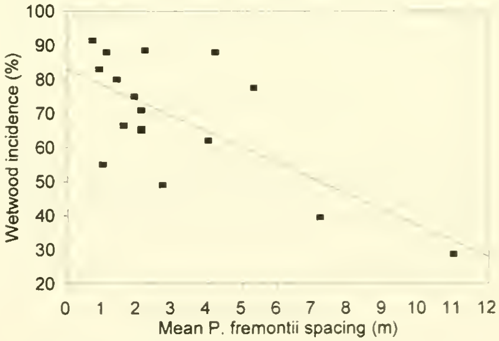

Fig. 3. Mean site incidence of wetwood symptoms in *Populus fremontii* (values averaged for size class 1 and 2 trees, dbh 1–64 cm) in relation to mean host spacing (i.e., density).

TABLE 3. Correlation coefficients between site variables and wetwood incidence and severity values for 2 size classes of *Populus fremontii* (see Table 2).

	Incidence class 1	Incidence class 2	Severity class 1	Severity class 2
Mean spacing of *P. fremontii*	−0.52**	−0.71**	−0.41*	NS
Substrate texture	−0.64**	NS	−0.65**	−0.46*
Channel stability	−0.52**	NS	−0.60**	NS
Stream flow frequency	NS	NS	−0.47*	NS
Stand composition	NS	−0.42*	NS	−0.58**
Bark beetle incidence	NS	NS	0.43*	NS

**$P < 0.05$
*$P < 0.10$
NS = $P > 0.10$

TABLE 4. Multiple regression coefficients between site variables and wetwood incidence and severity values for 2 size classes of *Populus fremontii* (see Table 2).

Dependent variable	Independent variables	r^2
Incidence, class 1	Substrate texture	0.42
Severity, class 1	Substrate texture	0.44
Incidence, class 2	*P. fremontii* spacing	0.48
	P. fremontii spacing + stand composition	0.58
Severity, class 2	Stand composition	0.30

Given the quantitative relationship expressed between wetwood symptom bleeding severity and canopy decline, wetwood is ecologically significant for *P. fremontii* riparian communities. Such a relationship has not been previously reported for any host species and has potential consequences (positive and negative) for insect and bird species that variously depend on live or dead cottonwood canopy for habitat. Canopy decline may ultimately lead to tree death. Further study of wetwood incidence and severity in relation to biotic integrity of *P. fremontii* communities is warranted.

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BLOW FLIES (DIPTERA, CALLIPHORIDAE) OF IDAHO: AN ANNOTATED CHECKLIST

Donald R. Brothers[1]

ABSTRACT.—A total of 33 species of blow flies (Diptera: Calliphoridae) are recorded from Idaho. They include 1 species each of *Cochliomyia, Phormia, Protophormia, Trypocalliphora, Cyanus, Cynomya,* and *Melanodexia;* 12 species of *Protocalliphora;* 5 species of *Lucilia;* 6 species of *Calliphora;* and 3 species of *Pollenia.* Other calliphorid species that may also occur in the state include 5 species of *Protocalliphora* and 3 species of *Calliphora.* Known distribution, periods of activity, abundance within the state, and biological notes are provided.

Key words: Diptera, Calliphoridae, blow flies, Idaho, distribution.

Many blow flies (Diptera: Calliphoridae) are of economic importance because of their effects on public health (James 1947, Greenburg 1971), livestock (Williams et al. 1985), and wildlife (Baumgartner 1988, Sabrosky et al. 1989). In addition, an interest in blow flies as forensic indicators has become increasingly popular in recent years (Smith 1986, Greenburg 1991, Catts and Goff 1992). Therefore, information about these flies is important.

In 1948, Hall's monograph, *The blowflies of North America,* provided comprehensive coverage of the calliphorid fauna. Hall (1965) cataloged the blow flies in *A catalog of the Diptera of America north of Mexico,* Cole (1969) included information about the family in his general work on western flies, and Shewell (1987) provided identification keys, illustrations, and brief comments pertaining to Nearctic species. From the Rocky Mountain states and westward, only 2 works cover the blow flies at the state level, James (1955) for California and De Jong (1994) for Colorado. This work adds to localized knowledge by providing information about the distribution, periods of activity, abundance, and biology of blow flies known to occur or which may occur in Idaho. This checklist is a preliminary step toward a more detailed publication on Idaho blow flies (primarily on synanthropic species) containing biological notes, identification keys, and illustrations.

The present records are based on intermittent collections by the author throughout much of Idaho since 1968 utilizing general collecting techniques and fly traps, sweeping over bait stations and road-killed animals, and rearing to adults larvae taken from carcasses; literature reports by Hall (1948), Linam and Rees (1957), Horning and Barr (1970), and Sabrosky et al. (1989); and specimens examined by the author from the following institutions: U.S. National Museum of Natural History (Systematic Entomology Laboratory, Agricultural Research Service, USDA), Smithsonian Institution (USNM), University of Idaho (WFBM), Albertson College of Idaho (CIDA), Washington State University (WSUC), Utah State University (EMUS), and Brigham Young University (BYUC). Excluding the genera *Protocalliphora, Trypocalliphora,* and *Melanodexia,* voucher specimens of 17 species from the author's collection have been deposited at USNM.

The taxonomic contribution of Rognes (1991) suggests that the synonymy of Hall (1965) and Shewell (1987) for North American calliphorids is out of date. Therefore, the arrangement of genera and species in this text is as presented by Rognes (1991) and subsequently listed for the Nearctic region by Poole (1996). Species are listed alphabetically within genera. Because of long-standing use in earlier works, some generic and specific names are included in this list for reference. An asterisk (*) identifies calliphorid species which currently are not reported from Idaho but which may occur in the state based

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on collection records in proximity to state boundaries. Periods of activity are based on earliest and latest collection dates in the calendar year. Abundance is based on relative abundance at collection sites.

SUBFAMILY CHRYSOMYINAE

Genus *Cochliomyia* Townsend

Cochliomyia macellaria **(Fabricius).** Canyon, Oneida, and Washington counties. August–October. Rare. The Canyon County record involved myiasis in a dog (O'Keeffe 1970), and the Washington County record involved myiasis in a human (Portman 1954).

Genus *Phormia* Robineau-Desvoidy

Phormia regina **(Meigen).** Ada, Adams, Bannock, Blaine, Boise, Bonner, Bonneville, Butte, Camas, Canyon, Cassia, Clark, Custer, Elmore, Franklin, Gem, Gooding, Idaho, Jefferson, Kootenai, Latah, Lemhi, Lewis, Nez Perce, Oneida, Owyhee, Shoshone, Teton, Twin Falls, Valley, and Washington counties. January–November. Very common. Adults overwinter. This species is generally the 1st fly species to appear at a fresh carcass and will be the most common species at the carcass initially. The fly is often involved in wound myiasis and sheep strike (James 1955).

Genus *Protocalliphora* Hough

All species of *Protocalliphora* are parasitic on birds. Because adults are not typically attracted to carrion (which is normally a major source of blow flies), adults of all species are scarce in collections and are not commonly observed in nature. Sabrosky et al. (1989) provides the sole source of information for species records included in this checklist.

Protocalliphora aenea **Shannon and Dobroscky.** Shoshone County. Known hosts that occur in Idaho include American Dipper, Say's Phoebe, American Robin, Barn Swallow, and House Wren.

Protocalliphora avium **Shannon and Dobroscky.** Ada, Bear Lake, Franklin, Nez Perce, Latah, Onedia, and Owyhee counties. This species is parasitic on the American Crow and raptorial birds.

Protocalliphora beameri **Sabrosky, Bennett, and Whitworth.** Butte County. This species is known only to parasitize swallows.

Protocalliphora brunneisquama **Sabrosky, Bennett, and Whitworth.** Butte County. Only known host of this species is the Chipping Sparrow.

******Protocalliphora chrysorrhoea*** **(Meigen).** This species has been recorded in Cache County, Utah, and Ravalli County, Montana. The chief host is the Bank Swallow. This species probably occurs in Idaho.

Protocalliphora cuprina **(Hall).** Franklin County. Hosts include the dove and passeriform birds.

******Protocalliphora halli*** **Sabrosky, Bennett, and Whitworth.** This species has been recorded in Box Elder, Cache, and Rich counties, Utah, and in British Columbia. The chief hosts are Say's Phoebe and Barn Swallow. This species probably occurs in Idaho.

******Protocalliphora hesperia*** **Shannon and Dobroscky.** This species has been recorded in Box Elder and Cache counties, Utah, and in British Columbia. Known hosts include several passeriform birds. This species probably occurs in Idaho.

Protocalliphora hirundo **Shannon and Dobroscky.** Bear Lake, Bonner, and Custer counties. Although chief hosts are swallows, several other passeriform birds are parasitized.

******Protocalliphora interrupta*** **Sabrosky, Bennett, and Whitworth.** Recorded from Cache County, Utah, and British Columbia. Known hosts are chiefly Yellow-headed, Brewer's, and Red-winged Blackbirds, Song Sparrow, and Marsh Wren. This species probably occurs in Idaho.

Protocalliphora lata **Sabrosky, Bennett, and Whitworth.** Franklin County. Known hosts include Red-tailed Hawk, American Kestrel, and Northern Goshawk.

Protocalliphora metallica **(Townsend).** Caribou, Latah, and Oneida counties. Known hosts include numerous passeriform species.

******Protocalliphora parorum*** **Sabrosky, Bennett, and Whitworth.** Recorded from Box Elder and Cache counties, Utah. Known hosts are chiefly chickadee species. This species probably occurs in Idaho.

Protocalliphora seminuda **Sabrosky, Bennett, and Whitworth.** Butte and Oneida counties. Known hosts include Brewer's Blackbird, Horned Lark, and Barn Swallow.

******Protocalliphora shannoni*** **Sabrosky, Bennett, and Whitworth.** Recorded from Cache County, Utah; Ravalli County, Montana; and near Vernon, British Columbia. Known hosts include a number of passeriform birds. This species probably occurs in Idaho.

Protocalliphora sialia **Shannon and Dobroscky.** Bear Lake, Franklin, and Latah counties. Known hosts include numerous passeriform species.

Protocalliphora spatulata **Sabrosky, Bennett, and Whitworth.** Latah County. Sabrosky et al. (1989) reported Rosy Finch, Horned Lark, and Water Pipit as hosts. Fair and Miller (1995) added Savannah Sparrow and White-crowned Sparrow.

Protocalliphora spenceri **Sabrosky, Bennett, and Whitworth.** Nez Perce County. Known hosts include American Redstart, Warbling Vireo, Yellow Warbler, and Slate-colored Junco.

Genus *Protophormia*
Townsend

Protophormia terraenovae **(Robineau-Desvoidy).** Ada, Adams, Benewah, Blaine, Boise, Bonner, Bonneville, Butte, Camas, Canyon, Cassia, Clark, Custer, Elmore, Franklin, Fremont, Gem, Idaho, Jefferson, Latah, Lemhi, Lincoln, Nez Perce, Oneida, Shoshone, Twin Falls, and Valley counties. January–October. Common. This species overwinters as adults. It is most abundant during the spring and fall.

Genus *Trypocalliphora*
Peus

Trypocalliphora braueri **(Hendel).** Hall (1965) and Sabrosky et al. (1989) placed the species in the genus *Protocalliphora*. Nez Perce and Oneida counties. Known hosts include Golden Eagle and passeriform birds. Maggots of this species are often found beneath the skin, causing true myiasis (Sabrosky et al. 1989).

SUBFAMILY LUCILIINAE

Genus *Lucilia*
Robineau-Desvoidy

Lucilia elongata **Shannon.** Hall (1965) placed the species in the genus *Bufolucilia*. Elmore County. Rare. The single specimen from Idaho was collected 22 August 1974 in the Trinity Lakes area. James and Maslin (1947) and Briggs (1975) reported the species as a parasite on toads.

Lucilia illustris **(Meigen).** Ada, Adams, Bannock, Benewah, Blaine, Boise, Canyon, Custer, Elmore, Franklin, Gem, Gooding, Idaho, Latah, Lemhi, Lewis, Nez Perce, Shoshone, Twin Falls, and Valley counties. April–November. Common. Although this is primarily a silvan species, in Idaho the species is a competitor with *L. sericata* for decaying meat and carrion in many cities.

Lucilia sericata **(Meigen).** Hall (1965) placed the species in the genus *Phaenicia*. Ada, Adams, Bannock, Bingham, Blaine, Boise, Bonneville, Camas, Canyon, Cassia, Custer, Elmore, Jefferson, Jerome, Latah, Nez Perce, Owyhee, Twin Falls, and Washington counties. April–September. Very common. This species is the most common metallic-colored fly in residential communities. Food range of the larva is wide, enabling it to develop commonly in garbage.

Lucilia silvarum **(Meigen).** Hall (1965) placed the species in the genus *Bufolucilia*. Ada, Bonneville, Camas, Canyon, Cassia, Elmore, Franklin, Fremont, Gem, Jerome, Latah, Lincoln, Madison, Minidoka, Nez Perce, Oneida, Owyhee, and Twin Falls counties. April–November. Moderately common. Although recognized as parasitic on frogs and toads (Hall 1948, Bleakney 1963), Brothers (1970) found the species to be more commonly a saprophage.

Lucilia thatuna **Shannon.** Hall (1965) placed the species in the genus *Bufolucilia*. Ada, Boise, Idaho, Latah, Nez Perce, and Washington counties. May–September. Scarce. The biology of this fly is not known.

SUBFAMILY CALLIPHORINAE

Genus *Calliphora*
Robineau-Desvoidy

******Calliphora alaskensis*** **(Shannon).** Hall (1965) placed the species in the genus *Acronesia*. Recorded from Lake Junction, Yellowstone National Park, Wyoming, during the month of August 1927 (Hall 1948). This fly probably occurs in Idaho as a rare species.

******Calliphora aldrichia*** **(Shannon).** Hall (1965) placed the species in the genus *Acronesia*. Recorded from Lake Junction and Old Faithful, Yellowstone National Park, Wyoming, during August 1927 (Hall 1948). Although rare throughout its range (Alaska to Colorado), this species probably occurs in Idaho.

Calliphora coloradensis **Hough.** Blaine, Boise, Butte, Gooding, Teton, and Valley counties. June–September. Uncommon.

******Calliphora grahami*** Aldrich. Hall (1965) placed the species in the genus *Aldrichina*. Recorded from Logan Canyon, Cache County, Utah, from a single specimen collected 9 July 1954. Introduced from China, this species has spread from California since the 1930s to half a dozen western states (James 1955). The species probably occurs in Idaho.

Calliphora lilaea **(Walker).** Hall (1965) placed the species in the genus *Eucalliphora*. Ada, Adams, Bannock, Blaine, Boise, Bonner, Butte, Camas, Canyon, Caribou, Cassia, Clearwater, Custer, Elmore, Gem, Gooding, Idaho, Jerome, Latah, Lemhi, Lewis, Lincoln, Nez Perce, Oneida, Owyhee, Shoshone, Teton, and Twin Falls counties. January–December. Common. Adults of this species overwinter. It is the most common of the "blue bottle" flies attracted to carrion in the early spring.

***Calliphora livida* Hall.** Ada, Blaine, Butte, Camas, Elmore, Latah, and Kootenai counties. January–December. Uncommon.

***Calliphora terraenovae* Macquart.** Ada, Adams, Blaine, Boise, Boundary, Camas, Cassia, Lewis, Lemhi, Nez Perce, Oneida, and Twin Falls counties. February–December. Moderately common.

***Calliphora vicina* Robineau-Desvoidy.** Ada, Blaine, Boise, Bonneville, Butte, Canyon, Gem, Nez Perce, Payette, and Washington counties. April–December. Moderately common.

***Calliphora vomitoria* (Linnaeus).** Ada, Blaine, Boise, Bonner, Butte, Camas, Cassia, Custer, Elmore, Franklin, Gem, Kootenai, Latah, Lewis, Nez Perce, Oneida, and Valley counties. April–October. Especially common during the fall of the year.

Genus *Cyanus*
Hall

***Cyanus elongata* (Hough).** Hall (1965) reported the species as *elongatus*. Boise, Canyon, Latah, Oneida, and Owyhee counties. May–November. Rare. Little is known about the biology of this species. Specimens collected in Boise County in September were on broken melons in a garden.

Genus *Cynomya*
Robineau-Desvoidy

***Cynomya cadaverina* Robineau-Desvoidy.** Hall (1965) placed the species in the genus *Cynomyopsis*. Ada, Adams, Blaine, Boise, Boundary, Butte, Camas, Canyon, Caribou, Cassia, Custer, Franklin, Fremont, Gem, Idaho, Latah, Lewis, Nez Perce, Oneida, and Owyhee counties. April–December. Moderately common. In addition to being attracted to carrion, this species is also attracted to human and dog excrement and fermenting fruit.

Genus *Melanodexia*
Williston

***Melanodexia idahoensis* (Hall).** Latah County. May. Rare. Repeated visits to the vicinity of the type locality during May by the author have produced no specimens. Nothing is known about the biology of this species.

Genus *Pollenia*
Robineau-Desvoidy

Hall (1965) listed 2 species of the genus *Pollenia* in North America, the widespread *rudis* (Fabricius) and the European *vagabunda* (Meigen) from British Columbia, the latter species being reported by Shewell in 1961. Rognes (1987, 1991, 1992) expanded the number of species to 5. At least 3 occur in Idaho. However, specimens in most collections checked have not been reviewed in light of the more recent classification. Therefore, distribution of the species in the state is uncertain. Data presented for the 3 reported Idaho species are based only on a limited number of specimens in the author's collection. In general, species of this genus have been collected in nature statewide from January to October. These flies are parasites of earthworms (Yahnke and George 1972, Thomson and Davies 1973). They can be a common pest during the winter in buildings where they overwinter.

***Pollenia angustigena* Wainwright.** Boise County. January, March.

***Pollenia pediculata* Macquart.** Rognes (1987) reported the species as *P. pseudorudis* Rognes. Ada County. July–October.

***Pollenia rudis* (Fabricius).** Ada and Boise counties. February–October.

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NEW DISTRIBUTIONAL RECORDS FOR SPOTTED BAT *(EUDERMA MACULATUM)* IN WYOMING

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ABSTRACT.—Before 1990 the spotted bat (*Euderma maculatum*) was known in Wyoming from only 2 records. Between June 1994 and May 1997 we documented habitat use and observations incidental to conducting a bat inventory of caves and abandoned mines. By monitoring audible echolocation calls, we observed bats at mist-netting sites. Spotted bats were heard or captured on 13 nights at 10 locations, all of which were near canyons or high cliff faces. No foraging habitat preferences were noted. *E. maculatum* occurrence appears to be related to roost structure, roost availability, and proximity to a permanent water source.

Key words: Euderma maculatum, *spotted bat, bat, echolocation, audible calls, Wyoming.*

The spotted bat (*Euderma maculatum*) is a relatively large bat (forearm = 48–51 mm, weight = 16–20 g) with striking coloration. There are 3 large white spots, 2 in the shoulder region and 1 on the rump, against a black dorsal surface, and the ventral surface is light with dark underfur. The ears, larger than those of any other North American bat, and wing membranes have a pink cast. Average external measurements are total length, 126 mm; tail, 51 mm; hind foot, 12 mm; ear, 47 mm (Schmidley 1991).

The spotted bat has been reported occurring in a wide variety of habitats, from desert shrub to coniferous forest (Findley and Jones 1965). Early records seemed to indicate a preference for forested habitat (Vorhies 1935) or caves (Vorhies 1935, Hardy 1941, Parker 1952). However, recent data indicate roosting habitat is rocky cliffs (Watkins 1977, Leonard and Fenton 1983). Spotted bats were never observed more than 10 km from substantial cliff features in California research (Pierson and Rainey 1998). Pierson and Rainey (1998) found spotted bats in black oak, ponderosa pine, incense cedar, giant sequoia/red fir, lodgepole pine, and white fir habitats in California. However, spotted bats have been observed or captured most often in dry, desert terrain at low elevations, often in association with a variety of habitats in canyon bottoms (Storz 1995). Foraging has been observed in forest openings (Woodsworth et al. 1981), pinyon juniper woodlands and large riverine/riparian habitat (Navo et al. 1992), meadows (Storz 1995), and wetlands and old agricultural fields (Leonard and Fenton 1983, Wai-Ping and Fenton 1989, Worthington 1991, Pierson and Rainey 1998).

Prior to 1990, *E. maculatum* was documented in Wyoming by a single specimen found dead near Byron (Mickey 1961). This specimen, originally deposited in the University of Wyoming mammal teaching collection, has since been misplaced and apparently lost. A photograph taken of a living individual at the Bighorn National Recreation Area headquarters near Lovell (Clark and Stromberg 1987) represents the 2nd Wyoming record. Both specimens were from the Bighorn Basin of north central Wyoming. We report an additional 34 observations, 31 audible calls (an audible call represents 1 pass), and 3 captures from 10 locations in Wyoming (Fig. 1). One capture and 1 call, possibly representing 2 different bats, occurred inside a cave.

The exact locations of *E. maculatum* observations reported at or near hypogeal bat roost sites are not reported due to the potential for human disturbance (Sheffield et al. 1992). Locations are available from the authors upon written request.

METHODS

Captures, sightings, and habitat use by *E. maculatum* were documented incidental to

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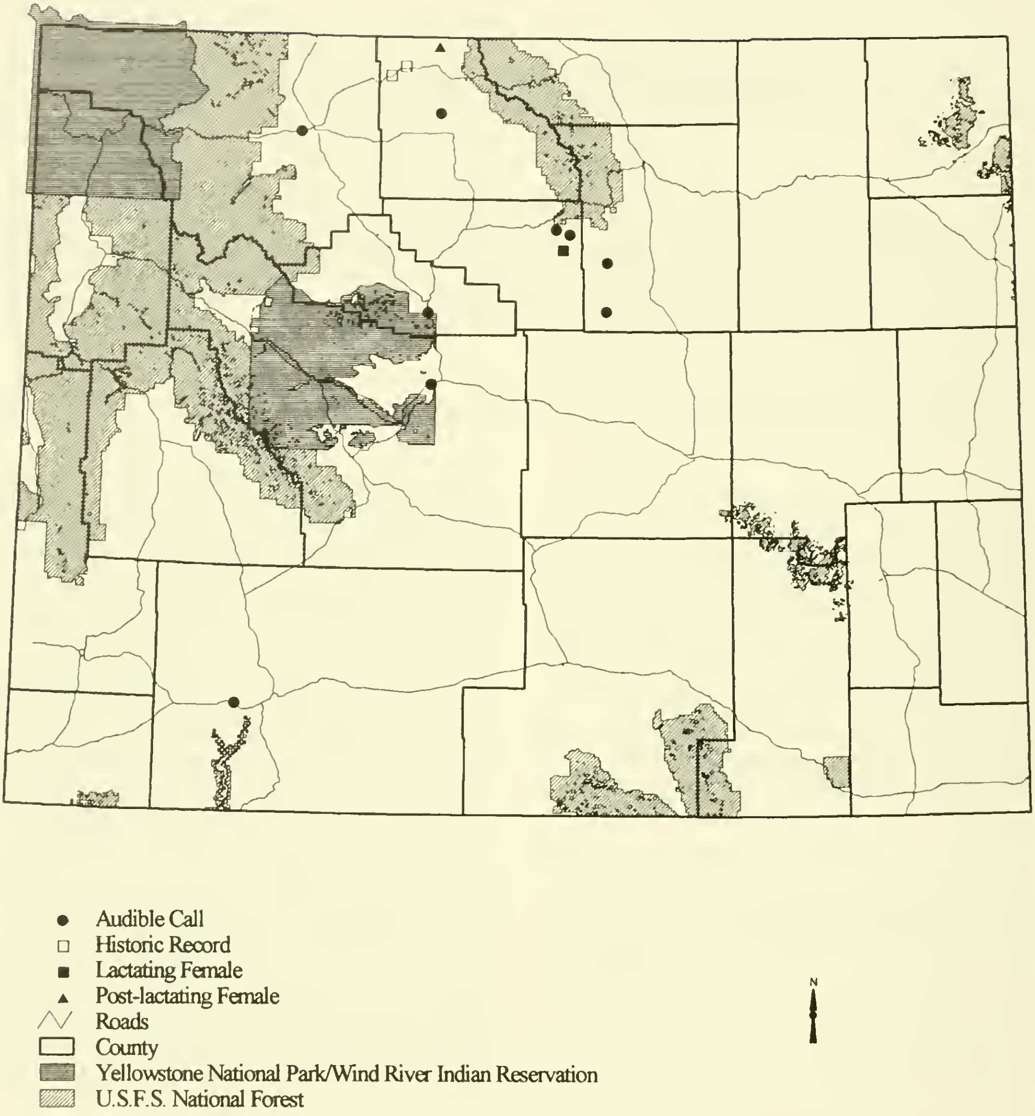
● Audible Call
□ Historic Record
■ Lactating Female
▲ Post-lactating Female
Roads
County
Yellowstone National Park/Wind River Indian Reservation
U.S.F.S. National Forest
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Fig. 1. Historic records, capture locations (1990, 1994), and audible calls (1990, 1994–95) of spotted bat (*Euderma maculatum*) in Wyoming.

conducting bat surveys near caves and abandoned mines and cannot be considered a survey for the spotted bat. *E. maculatum* were either captured by mist-nets or identified by audible calls. We defined an audible call as either the series of clicking sounds emitted by *E. maculatum* in-flight while searching for insects, or rapid feeding buzzes. Each pass of a single bat was defined as 1 audible call. *E. maculatum* has the lowest frequency echolocation call of any bat found in Wyoming and is the only Wyoming bat with an echolocation call audible to the human ear.

Species that occur in the United States and have audible echolocation calls include *Idionycteris phyllotis*, *Nyctinomops macrotis*, and *Euderma maculatum*. Fenton and Bell (1981) reported the range of *I. phyllotis* as 12–24 kHz. The call of *Nyctinomops* (*Tadarida*) *macrotis* ranges from 17 kHz to 25 kHz (Simmons and O'Farrell 1977), and *E. maculatum* ranges from 9 kHz to 15 kHz (Leonard and Fenton

1984). *N. macrotis* has been reported from Wyoming on only 1 occasion and is considered a Neotropical species occurring from central Colorado into Mexico, while *I. phyllotis* occurs from extreme southwestern Colorado into Mexico (Fitzgerald et al. 1994). *Antrozous pallidus*, which uses audible vocalizations to communicate intraspecifically, has been captured by the authors a number of times in Wyoming; thus, calls of this species and *E. maculatum* were separated by experience and comparison to calls heard immediately prior to the capture of 3 individual *E. maculatum*. Audible monitoring consisted of sitting quietly at a predetermined location and listening for calls during the entire survey period.

Sites in which *E. maculatum* was captured or audible calls were detected are listed. Legal descriptions are given for sites 1, 3, and 7 since they are not adjacent to caves and thus are not susceptible to disturbance by humans. Habitats are included but foraging cannot be assumed since feeding buzzes were not detected at all sites.

SITE 1.—We conducted a bat mist-netting survey in extreme northern Wyoming, T57N, R94W, S2, SWNE, Little Mountain Plateau, 19.3 km NE of Lovell, Bighorn County, on the nights of 27 and 28 August 1990. The survey site is 5.6 km E of Bighorn Canyon, a deep canyon with high rock walls. Habitat includes juniper (*Juniperus scopulorum*) and open grassland. Two shallow ponds approximately 75 m and 115 m, respectively, from a small spring were covered with a mist-net configuration. On the 1st night the pond closest to the spring had one 9.1-m mist-net set diagonally across the pond. On the pond farthest from the spring, four 9.1-m mist-nets were set, 3 in a "Z" pattern across the pond, and 1 on the edge of the pond perpendicular to the Z. On the 2nd night, each pond had three 9.1-m mist-nets set in a Z pattern. Mist-nets were continuously monitored from 2030 h to 2330 h on both nights and left in place without monitoring until daylight (0530 h), at which time they were checked.

SITE 2.—A cave in Spring Creek Canyon, 21 km SE of Tensleep, Washakie County, was surveyed on 17 July 1994. It is located on the south side of the canyon 200 m upslope from the base of a sheer limestone cliff. The 4.8-km-long canyon has high, shear rock faces and contains a small perennial stream. Boxelder (*Acer negundo*) occurs near the stream banks, with mountain mahogany (*Cercocarpus montanus*), big sagebrush (*Artemisia tridentata*), and *J. scopulorum* between the stream and canyon rim. The cave entrance is 23.7 m wide × 7.6 m high. The passage (110 m) contains 3 rooms and varies in size, 7.6–23.7 m in width and 3–9.1 m in height. A 2.1 × 2.4-m mist-net was placed at the entrance to the 2nd room (passage size 6.1 × 3 m), approximately 15.2 m inside the cave, and monitored every 15 min during the period 2030 h to 2345 h.

SITE 3.—Canyon Creek, T47N, R87W, S27, 12.9 km E of Tensleep, Washakie County, was surveyed on 18 July 1994 between 2100 h and 2400 h. Elevation is 1524 m. Canyon Creek is a perennial stream in a canyon of rugged rock outcrops and steep canyon walls. Adjacent habitat is mixed *J. scopulorum* and *A. tridentata*.

SITE 4.—The survey site located 3.2 km NW of the town of Green River, Sweetwater County, was surveyed on 21 July 1994 from 2100 h to 0115 h on 22 July. Elevation is 1890 m. Steep, rugged canyons with bare rock walls contain cracks and fissures. The Green River is approximately 0.8 km S of the cave. Greasewood (*Sarcobatus vermiculatus*) occurs between the river and cliffs, with *A. tridentata* on the plateau.

SITE 5.—A canyon located 5.6 km SW of Cody, Park County, was surveyed on 5 August 1994 from 2030 h to 2400 h. Elevation is 1920 m. The terrain is characterized by steep canyons and shear rock faces. Adjacent habitat is Douglas-fir (*Pseudotsuga menziesii*) interspersed with limber pine (*Pinus flexilis*) and aspen (*Populus tremuloides*).

SITE 6.—An area of natural caves and high, bare rock walls in Wind River Canyon 8.0 km S of Thermopolis, Hot Springs County, was surveyed on 6 June 1995 from 2030 h to 2300 h. Elevation is 1345 m. Habitat is mixed *A. tridentata* and *J. scopulorum*, with sagebrush-grassland on the plateau.

SITE 7.—Sheep Canyon, T54N, R94W, S35, NE, along the Bighorn River 7.2 km NW of Greybull, Big Horn County, was surveyed on 20 June 1995 from 2000 h to 2300 h. Elevation is 1250 m. Sheer rock exists between the river and the rim. Mixed sagebrush-grassland occurs on the plateau.

SITE 8.—This karst area with high, bare rock walls along the Middle Fork of the Powder

TABLE 1. Location, date, and hour of *E. maculatum* captures and calls in Wyoming, 1990–1995.

Site #	Date	Time interval of calls	Number of captures	Number of audible calls
1	27–29 August 1990	2030–2330	2	5
2	17 July 1994	2150–2212	1	4
3	18 July 1994	2150–0018		4
4	21 July 1994	2145–2222		3
	1 August 1994	2135		1
5	5 August 1994	2135		1
6	6 June 1995	2142		1
	7 August 1995	2301		1
7	20 June 1995	2350–0008		5
8	20 July 1995	2112–2122		4
9	28 August 1995	2111		1
10	16 October 1995	1900		1
TOTAL			3	31

River 10.5 km SW of Barnum, Johnson County, was surveyed on 20 July 1995 from 2030 h to 2300 h. Elevation is 1597 m. Narrowleaf cottonwood (*Populus angustifolia*) and *A. negundo* occur near the stream banks, with lodgepole pine (*Pinus contorta*), *J. scopulorum*, and *A. tridentata* between the river and canyon rim. The plateau is dominated by sagebrush-grassland with scattered *P. contorta*.

SITE 9.—A karst area 12.9 km W of Mayoworth, Johnson County, was surveyed on 28 August 1995 from 2000 h to 2300 h. Elevation is 2530 m. The site is located in an area of mixed *P. contorta* and *P. menziesii* interspersed with open sagebrush-grassland parks. Rock outcrops and a canyon with bare rock walls occur within 1.6 km of the survey site. Three man-made stock ponds occur within 3.2 km.

SITE 10.—The survey site 6.4 km SW of Shoshoni, Fremont County, was surveyed on 16 October 1995 from 2000 h to 2100 h. The site is on the eastern shoreline of Boysen Reservoir near several high rock bluffs in sagebrush-grassland. Elevation is 1460 m.

RESULTS

Spotted bats were captured on 3 occasions and audible calls were documented 31 times between 1990 and 1995 (Table 1).

At site 1 five calls of *E. maculatum* were heard on 27 August 1990 between 2030 h and 2330 h. One post-lactating adult female was captured in a mist-net set between 2330 h on 27 August and 0600 h on 28 August. A 2nd adult post-lactating female was captured at the same site between 2230 h on 28 August and 0600 h on 29 August. Both specimens (BS/FC 14512 and BS/FC 14513, respectively) were retained and reported under Mike Bogan's collection permit and are currently deposited in the Biological Surveys Collection, Museum of Southwestern Biology, University of New Mexico, Albuquerque.

At site 2 a lactating female *E. maculatum* was captured in the mist-net at 2200 h on 17 July. *E. maculatum* calls were heard at 2150 h, 2155 h, 2206 h, and 2212 h. Three calls were heard outside the cave, while the 4th occurred 9.1 m inside the cave near the mist-net location. It is not known whether the bats intended to night roost, were foraging inside the cave, or were merely investigating the site. Storz (1995) and Leonard and Fenton (1983) documented *E. maculatum* activity throughout the night. The timing of audible calls documented at 9 sample sites in Wyoming is shown in Table 1. Sampling did not occur after 0018 h; however, for the summer (June through August), audible calls were documented throughout the period 2030 h to 0018 h. The mean time at which the first call was documented was 2200 h, indicating that foraging begins in early evening.

DISCUSSION

Eighty-two survey nights resulted in *E. maculatum* being captured or identified by audible calls on 13 nights at 10 locations. Fenton et al. (1987) reported no obvious association between spotted bat occurrence and a particular habitat type. However, all recorded occurrences of *E. maculatum* in Wyoming were associated with canyons containing cracks and fissures, high bare rock walls, and rock ridges close to a permanent water source. Our observations indicate *E. maculatum* to be more closely associated with structure and roost availability than specific vegetation types. Our observations support those of Easterla (1970), Wai-Ping and Fenton (1989), Navo et al. (1992), and Storz (1995), and indicate that *E. maculatum* is not restricted by foraging habitat or geographic location in Wyoming. As reported for Colorado and Utah (Storz 1995), populations of *E. maculatum* appear locally abundant in areas with available roosting habitat and are absent from areas without suitable roost structure even though habitat is otherwise suitable.

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SOREX MONTICOLUS IN SHRUB STEPPE HABITAT IN THE NORTHERN GREAT BASIN

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Key words: Sorex monticolus, *shrub steppe, Idaho, Owyhee, montane habitat, biogeography, shrew,* Artemisia tridentata.

Sorex monticolus occurs from northern Alaska to northwestern Mexico and from the Pacific coast to the western edge of the Great Plains (Smith and Belk 1996). It is commonly found in high-elevation spruce-fir forest, alpine tundra, and mid-elevation Douglas-fir–pine forests throughout most of its range, and pinyon-juniper woodlands in the northern Great Basin (Hennings and Hoffmann 1977). We report herein the 1st record of *S. monticolus* in Owyhee Co., Idaho, and briefly discuss some implications of its occurrence in the shrub steppe habitat of the northern Great Basin.

While conducting small mammal surveys, we used 3 × 3 × 10″ Sherman live-traps baited with oatmeal and millet and placed them in 5 × 5 trap grids in various shrub steppe vegetation communities. We separated all traps by 15 m. On each of 2 consecutive nights (31 October and 1 November 1996) we captured 1 *S. monticolus* in shrub steppe habitat in different traps adjacent to one another. The capture site was at an elevation of 1792 m in Owyhee Co., Idaho, approximately 140 km south of Boise (Fig. 1). We found both shrews dead in the traps the mornings following trapping. Some patches of snow covered the ground during the survey period, and ambient temperatures during the 2 nights of trapping ranged from –6° C to +1° C.

Shrub steppe vegetation in the area is generally characterized by large expanses of low sagebrush (*Artemisia arbuscula*) surrounding patchily distributed "islands" of tall-shrub communities found in areas of greater moisture (i.e., north-facing slopes and lee sides of hills where snowpack accumulates in the winter). We captured the shrews in a trapping grid located in a tall-shrub (ca 1.5 m) island dominated by big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*). Herbaceous understory in the area is composed of both perennial and annual grasses and a variety of post-senesced forbs dominated by species of *Phlox*. We located the trapping grid on a 10% slope with a north aspect, where microbiotic crust consisting of mosses and lichen carpeted the ground below the shrubs and some litter in the form of dead branches was present. Compared to the surrounding area that has been exposed to moderate grazing, livestock impact in the trapping grid is minimal. Several ephemeral springs and drainages are located ca 1.6 km from the capture site, but riparian vegetation is absent and evidence of heavy livestock usage is apparent. The nearest perennial water source with riparian vegetation is located ca 3.2 km S at Crab Creek.

Eric Yensen of Albertson College of Idaho (AC) identified the specimens, which were prepared as standard study skins and skulls and deposited in the AC Museum of Natural History (ACMNH 1008 and 1009). The specimens were identified based on dentaries (Carraway 1995). The medial tines of the upper incisors of both specimens were large and located well below the upper limit of the red pigment. We confirmed the identifications by comparison to specimens of *S. monticolus* and *S. vagrans* in the ACMNH. The pelages of both *S. monticolus* were distinctly "dusky" as compared to specimens of *S. vagrans* from Owyhee Co., Idaho, in ACMNH, which were lighter and brownish. Both shrews were young females with no placental scars.

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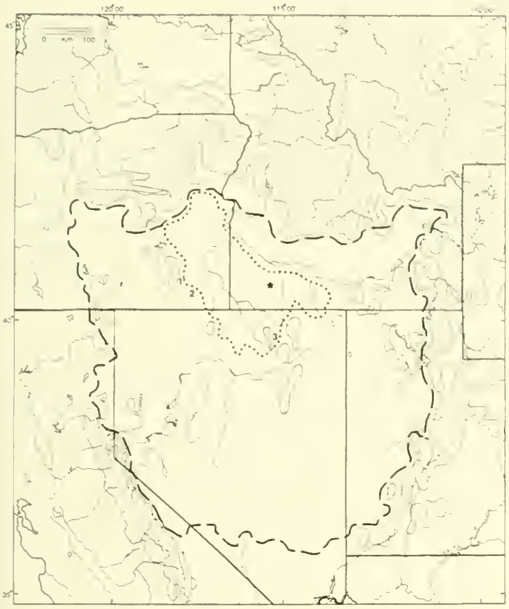

Fig. 1. Present capture site (star) and known geographic distribution of *Sorex monticolus* (stippled) in the Great Basin (dashed line) and the Owyhee Desert (dotted line) (adapted from Cronquist et al. 1972, Hennings and Hoffmann 1977, Alexander 1996, and Smith and Belk 1996). Numbers correspond to other occurrences of *S. monticolus* in shrub steppe (1 – Steens Mountain, 2 – Trout Creek Mountains, 3 – Independence Mountains).

Sorex monticolus, common in Idaho, is usually considered a montane species associated with high-elevation spruce-fir forests or alpine tundra (Zeveloff 1988, Alexander 1996). The capture site of these 2 specimens is located over 100 km from spruce-fir forests. Hennings and Hoffmann (1977) also report *S. monticolus* as occurring in pinyon-juniper woodlands in the northern Great Basin. Although juniper (*Juniperus occidentalis*) woodlands occur on the lower slopes of the Owyhee Mountains, Idaho (>40 km to N), and the Jarbidge Mountains, Nevada (>50 km to S), solitary junipers are widely distributed in the vicinity of the capture site.

While the occurrence of *S. monticolus* in shrub steppe habitat is not entirely unexpected, it is nonetheless unusual (K. Foresman personal communication). In the northern Great Basin, *S. monticolus* has been captured in tall-shrub associations in shrub steppe in southwestern Wyoming (Kirkland et al. 1997), northern Nevada (Ports and George 1990), and the slopes of the Steens and Trout Creek Mountains of southeastern Oregon (L. Alexander, E. Rickart, Utah Museum of Natural History: UU 28207, personal communication). All capture sites share flora common to the northern Great Basin, and the latter 3 sites somewhat delineate the periphery of the Owyhee Desert (Cronquist et al. 1972). The specimens constitute the 1st record of *S. monticolus* in Owyhee Co., Idaho (G. Stevens personal communication), and augment the number of occurrences of the species in shrub steppe habitat in the northern Great Basin.

S. monticolus use of shrub steppe may be due to several biotic (i.e., tall-shrub microhabitats) and abiotic (i.e., elevation and precipitation) factors common to the northern Great Basin. Ports and George (1990) suggested that shrews in the Great Basin may be very flexible in their foraging habits. Other studies have shown that besides dense ground cover, *S. monticolus* is weakly associated with physical or vegetation structure variables (Hawes 1977, Terry 1981, Doyle 1989, Belk et al. 1990). In addition, *S. monticolus* reportedly is less dependent on water and tolerates drier soils than the sympatric *S. vagrans* (Hennings and Hoffmann 1977). Flexibility in foraging habits, less reliance on a particular vegetation structure (i.e., high- to mid-elevation forests), and tolerance of xeric conditions may explain *S. monticolus* presence in shrub steppe habitat in the northern Great Basin.

Recent reports of the bushy-tailed woodrat (*Neotoma cinerea*) in the northern Great Basin (Grayson et al. 1996) have brought into question long-held assumptions on the distribution and habitat tolerance of alleged "montane" species. Furthermore, current static Great Basin small mammal biogeography models (i.e., "nested subset model"; Patterson and Atmar 1986) fail to adequately assess the wide range of geographical and biological variability that have produced the modern distribution of these species, especially in the northern Great Basin (Grayson et al. 1996). In the Great Basin, *S. monticolus*, like *N. cinereus*, has been considered a member of an assemblage of small mammals currently distributed on isolated mountain ranges (Brown 1971). The occurrence of *S. monticolus* in shrub steppe refutes this assumption and supports the call of Grayson et al. (1996) for a more dynamic view of Great Basin small mammal biogeography.

We suggest that S. *monticolus* may occur in shrub steppe habitat in the northern Great Basin more often than is currently thought and that shrews previously collected in the Owyhee Desert region may have been misidentified due to the difficulty of identifying species of the *vagrans-monticolus* complex (Hennings and Hoffmann 1977, Hall 1981, Woodward 1994).

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Mack, G.D., and L.D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. Journal of Wildlife Management 44:695–700.

Sousa, W.P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 *in* S.T.A. Pickett and P.S. White, editors, The ecology of natural disturbance and patch dynamics. Academic Press, New York.

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REPRODUCTIVE ECOLOGY OF BISON ON ANTELOPE ISLAND, UTAH

Michael L. Wolfe[1], Milan P. Shipka[2], and John F. Kimball[3]

ABSTRACT.—Autumn musters of bison (*Bison bison*) on Antelope Island State Park, Utah, conducted annually since 1987, provided data on temporal and age-specific reproductive patterns and a basis to evaluate the efficacy of management measures implemented to elevate reproductive performance in the herd. Pregnancy rates were variable and low ($\bar{x} = 46.2\%$) in comparison to other free-ranging, noncommercial bison herds in North America. Cows in the 3- and >6-yr age classes exhibited lower-than-expected pregnancy rates ($P < 0.05$). Annual pregnancy rates showed a significant ($r = 0.64$, $P = 0.047$) linear decline of 2.5% per annum. Variance in distribution of fetal ages observed in 6 yr indicates substantial temporal fluctuation. Long-term reproductive performance of cohorts born prior to implementation of management measures did not differ from that of cohorts born subsequent to these changes.

Key words: bison, Bison bison, *nutrition, reproduction, Utah, Antelope Island.*

A population of bison has existed on Antelope Island, Utah, for over a century. This herd originated from a very small ($n = 12$) founder population (Popov and Low 1950), and its subsequent population growth was punctuated by reduction to very low levels (i.e., <30 animals) on at least 2 occasions, increasing the potential of low levels of genetic variability and raising questions concerning possible demographic effects of the small founder population and subsequent bottlenecks. Preliminary field observations of reproductive patterns in the herd by Wolfe and Kimball (1989) revealed an unusually protracted calving period for this herd. Other reproductive anomalies may also exist. Alternative hypotheses to explain the long calving period are the absence of predation and a low-quality and temporally unpredictable forage resource.

Prior to 1981 Antelope Island State Park (AISP) encompassed only a small area at the north end of the island. In that year the Utah Division of Parks and Recreation (UDP&R) acquired the remainder of the island, including the bison herd, which was thought to number 250–280 animals. Initially, the population was subject to minimal management with the removal of only 3 male bison reported during the following 6-yr period.

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In 1987 the UDP&R initiated an active bison management program featuring annual musters, selective culling, inoculation of animals, artificial winter feeding of calves, and limited hunting of adult males. In 1987 grazing by approximately 1500 domestic cattle on the island was also terminated. The annual roundups provided an opportunity to collect information on reproductive patterns in the population and test hypotheses regarding the impact of these management changes on reproductive patterns within the population. Specifically, we hypothesized that a presumably improved nutritional plane resulting from the management program would increase reproductive rates and synchrony of parturition. Shipka et al. (1995) provided a preliminary analysis of the data obtained through 1992. This paper includes data collected subsequently and more comprehensive analysis.

STUDY AREA

Antelope Island has been described previously by Wolfe and Kimball (1989). Briefly, it is the largest (104 km^2) of several islands in the Great Salt Lake, lying approximately 6 km from the mainland. Topographically, the island is characterized by a north–south ridge (maximum elevation above lake level = 600 m) with steep west-facing escarpments and generally more gentle east-facing slopes.

Annual grasses constitute the principal vegetation on the island, with cheatgrass (*Bromus tectorum*) and threeawn (*Aristida* sp.) comprising the dominant taxa. These conditions are the result of range deterioration due to overgrazing, erosion, and recurrent wildfires (Jones 1985). Isolated pockets of juniper (*Juniperus osteosperma*) and big tooth maple (*Acer grandidentatum*) occur primarily on steeper slopes and canyons on the western side where they have been protected from fire. There are also limited stands of sagebrush (*Artemisia tridentata*) on some of these higher slopes. Some portions of the eastern slopes have been reseeded with perennial grasses and grass-legume mixtures.

Weather records for Antelope Island exist only for the period 1952–1972. During that interval annual precipitation averaged 39.3 cm, with snowfall of 25.1 cm. Average maximum summer (Jun.–Aug.) temperatures were 32.7°C, while minimum winter (Dec.–Feb.) temperatures were –6.2°C. Lower elevations on the island experience about 200 frost-free days annually, higher elevations about 150.

METHODS

The UDP&R has conducted an annual roundup of the Antelope Island bison herd in the last week of October or first week of November since 1987. These gatherings employ helicopters and ground support on horseback and in wheeled vehicles to haze the bison into large holding paddocks at the north end of the island. All animals in the herd are captured in the roundup or are at least accounted for during follow-up flights. Bison typically remain in the holding paddocks for approximately a week prior to being processed through a set of working chutes. During the period 1987–1997 this operation typically commenced on Julian day 309 and lasted 3–4 d.

Upon entering the squeeze chute, adult animals are identified and weighed. Every bison in the Antelope Island herd is permanently identified by means of metal ear tags, and calves are branded according to their birth year. Beginning in 1991, animals were also identified by means of microchip implants in their ears. Adult females were examined for pregnancy by rectal palpation. In 1987, 1988, 1990, 1992, 1993, and 1994 fetal age was estimated during pregnancy palpation.

During the 1987 roundup, provisional ages were assigned to younger animals based on the schedule of replacement of lacteal incisiform teeth (incisors and canines) as described by Hogben (in Larson and Taber 1980). The series of "known-age" cohorts established by marking calves of the current year provided the opportunity to verify this sequence and subsequently correct initial assignments of animals in the 1987 roundup through 4-yr-old age classes (Kimball and Wolfe 1989). The lingual-labial width of the central incisors (I_1) of most older bison was also measured during the 1987 and 1988 musters (Novakowski 1965). Further estimates of age were obtained by counts of cementum annulations in I_1 teeth collected from 32 animals (mortalities and hunter-killed animals). I_1-width data collected during the 1987 roundup were regressed against age estimates from cementum annulation counts and animals derived from known-age cohorts. For the purposes of this analysis, we established the following age categories: 2, 3, and 4 yr olds, 5–6 yr, and >6 yr.

Statistical analysis of reproductive data utilized procedures outlined by Cochran and Cox (1957) for categorical data. Two discrete categories (i.e., pregnant–not pregnant) were analyzed by chi-square procedures for a 2 × n contingency table using the following formula:

$$\chi^2 = \frac{\Sigma\, a_i p_i - \bar{p}\, \Sigma\, (a_i)}{(\bar{p})(\bar{q})}$$

where: a_i = number in category 1 within the ith age class,
$\bar{p}$ = overall proportion of the total population in category 1, and
$\bar{q} = 1 - \bar{p}$ = overall proportion of the total population in category 2.

This procedure allows for the examination of within-population differences when a known or expected value is not available. In addition, one-way ANOVA was used to evaluate the observed difference in pregnancy rates among various age classes with years being pooled. Differences between individual age classes were analyzed by means of Bonferroni *t* tests. Bartlett's test for homogeneity of variance was used to evaluate observed differences in the distribution of fetal ages.

RESULTS

Pregnancy Rates

Pregnancy determination for the period 1987–1997 indicated a mean annual pregnancy rate of 46.2% (range = 32.5–66.6%, Fig. 1). The rates observed in 1993 and 1997 were significantly higher (χ^2 = 40.9, df = 9, $P <$ 0.0005) and lower (χ^2 = 25.0, df = 9, $P <$ 0.005), respectively, than expected. Regression of annual pregnancy rates against time indicated an average annual decline of 2.5% (r = 0.64, P = 0.047). The value for 1987 was excluded from this analysis because we reasoned that pregnancy rates in that year were not affected by management changes described above. Regressions using pregnancy rates weighted by sample size and exluding the 1993 value, an "unusual" observation but not technically an outlier, yielded qualitatively similar results.

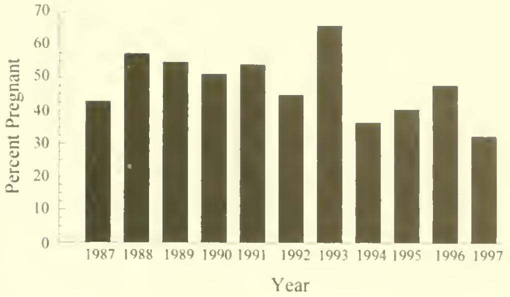

Fig. 1. Average annual pregnancy rates for Antelope Island bison cows ≥2 yr of age, 1987–1997.

We further tested the hypothesis that cohorts subject to the effects of management changes should have a higher reproductive rate than animals born before the changes were implemented. The long-term (≥ 5 yr of consecutive data) histories of females ≥ 2 yr of age and born during the period 1987–1991 were compared with similar performances of those females which had already achieved reproductive age in 1987 (Table 1). The mean long-term pregnancy rates of cows born during the 2 time intervals, 0.53 and 0.49, respectively, did not differ significantly (z = 0.46, P = 0.32). Likewise, maximum numbers of consecutive pregnancies between the 2 groups were virtually identical, 2.6 and 2.7, respectively (t = 0.35, P = 0.72).

One-way ANOVA revealed significant differences (F = 4.05, P = 0.007) among mean pregnancy rates for various age classes for the 11-yr period 1987–1997 (Fig. 1). Bonferroni *t* tests indicated that pregnancy rates in the 3- and >6-yr-old groups were significantly lower ($P < 0.05$) than the other age groups (Fig. 2).

Fetal Ages

Fetal ages were available for 6 yr of the study (Table 2) and indicated that 1988 had the lowest measures of central tendency with a suggestion of bimodal distribution. It should be noted, however, that the sample size in that year was less than half of the next lowest year. The results of Bartlett's test for homogeneity of variance suggested a tendency (P = 0.098) for this population to experience random fluctuations in the variance of fetal ages over time (Fig. 3).

TABLE 1. Reproductive performance of Antelope Island bison cows in relation to management changes.

Cohorts	Sample size (n)	Years observed ($\bar{x}$)	Pregnancy rate ($\bar{x} \pm s_{\bar{x}}$)	Maximum number of consecutive pregnancies ($\bar{x} \pm s_{\bar{x}}$)
Born before 1987	79	6.4	0.53 ± 0.06	2.7 ± 0.21
Born 1987–1991	61	6.5	0.49 ± 0.06	2.6 ± 0.18

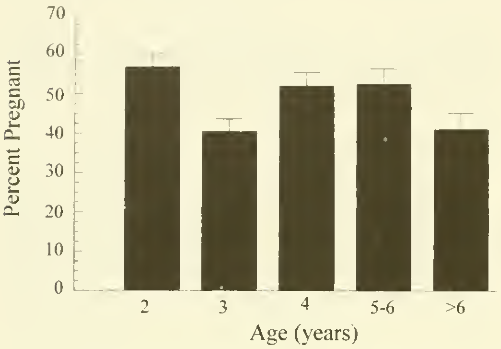

Fig. 2. Age-specific pregnancy rates of Antelope Island bison cows, 1987–1997.

Table 2. Summary statistics for estimated fetal ages of Antelope Island bison.

Year	Sample size	Age (days)		
		Median	$\bar{x}$	$s_{\bar{x}}$
1987	53	135	113.5	3.99
1988	31	105	103.1	7.08
1990	82	105	92.1	3.49
1992	61	135	121.2	3.26
1993	179	135	132.2	2.16
1994	106	135	120.7	2.90

DISCUSSION

Pregnancy rates in the AISP herd are low compared to some other free-ranging bison herds (Table 3). The only herd known to have a lower pregnancy rate than that on Antelope Island is the Santa Catalina herd. Lott and Galland (1987) suggested that the low reproductive rate in that herd was likely due to nutritional deficiency. Because forage quality appears to be low at the AISP location, that hypothesis may also be true for Antelope Island. Calves received supplemental winter feed during the latter portion of this study, which may have affected pregnancy rates among 2-yr-old cows. Puberty will be achieved at an earlier age, within a species group, among those individuals enjoying a higher plane of nutrition (Bronson 1989). An explanation for the lower-than-expected pregnancy rate among 3- and >6-yr-old animals is more elusive, however. Kirkpatrick et al. (1993) suggested that calving rates of 35–55% imply an every-other-year or every-third-year calving pattern. Whether this applies to Antelope Island bison is less certain, but some variant of less-than-every-consecutive-year pregnancy does operate. Approximately 1/3 of the females with known reproductive histories spanning intervals of 5–8 yr produced 2 calves during those intervals, while 23% and 11% produced a single calf or 3 calves, respectively. Only 13% gave birth to ≥ 5 calves.

Nutritional stress combined with metabolic requirements of lactation may limit the ability of first-calving bison cows to raise a calf and replenish body reserves sufficient to return to estrous cyclicity. Forage quality on Antelope Island is thought to be poor due to decades of overgrazing combined with erosion. Despite increased digestive efficiency by bison compared to cattle (DeLiberto 1993), poor forage quality may limit energy availability to young bison cows. Bronson (1989) showed that estrous cyclicity is related to whole body energy balance. Furthermore, suckling has a negative effect on the return to estrous cyclicity in domestic cattle (Short et al. 1990), and Kirkpatrick et al. (1993) have recently demonstrated, through physiological data, that lactational suppression of ovarian activity reduces fecundity in bison.

Wolfe and Kimball (1989) presented data on the apparently asynchronous calving pattern of the Antelope Island bison population in comparison to other herds (Meagher 1973, Haugen 1974, Rutberg 1986, Shaw and Carter 1989). They reported that calves were born from March through October, with 40% of the

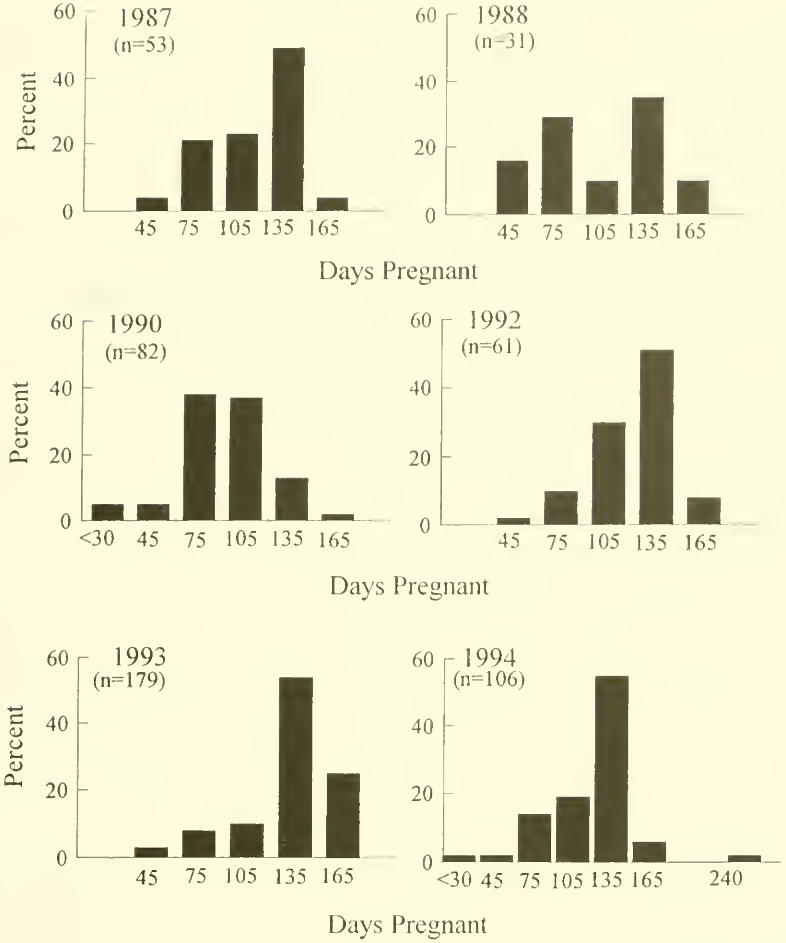

Fig. 3. Distribution of fetal ages in Antelope Island bison cows. Days pregnant refers to midpoints of monthly intervals as determined by rectal palpation.

births occurring from August through October. Green and Rothstein (1993) used the length of time from the first birth until 80% of the year's calves were born as a measure of birthing synchrony among bison in Wind Cave National Park (WCNP). Berger and Cunningham (1994) cited those data combined with data of Rutberg (1987) from the National Bison Range (NBR) and data collected from the Badlands National Park (BNP) bison herd, indicating that 80% of bison calves were born during 23, 49, and 55 days at NBR, WCNP, and BNP, respectively. Within the AISP bison herd, estimates of fetal ages by rectal palpation (Fig. 3) indicated more than 60 d spread in ages of the oldest fetuses in all 6 yr these data were collected. Additionally, during 3 of those 6 yr this interval was greater than 90 d in length. This extrapolates to an asynchronous period of parturition in comparison to the bison herds cited above, especially considering that the loss of any of those fetuses to abortion or resorption would only serve to lengthen this period during the calving season. Anecdotal reports by AISP personnel confirm the occurrence of very young (<3 months of age) calves as evidenced by their reddish tan coloration (Meagher 1979) during every month of the year.

Synchrony of parturition has been examined among populations of wild ungulates (Estes 1976, Rachlow and Bowyer 1991) and related to various causal mechanisms, namely predation effects and availability of forage. Bison

Table 3. Pregnancy rates of some free-ranging North American bison herds.

Location	Pregnancy rate (%)	Source
National Bison Range	88.2	Rutberg (1986)
Niobrara National Wildlife Refuge	78.4	Haugen (1974)
Witchata Mountains Wildlife Refuge	71.8	Shaw and Carter (1989)
Badlands National Park	64.3	Berger and Cunningham (1994)
Henry Mountains	63.0	Van Vuren and Bray (1986)
Yellowstone National Park	52.0	Meagher (1973)
Antelope Island	46.2	This study
Santa Catalina Island	35.0	Lott and Galland (1987)

herds at NBR, WCNP, BNP, and AISP are currently not subject to natural predators. Predation, other than hunting by humans, has not been a factor of consideration in any of these herds for at least 100 yr. In the absence of predation, environmental factors may become a more important determinant affecting synchronous parturition. Berger (1992) suggested that natural selection would still favor animals that calve at some optimal time that is linked to the annual peak bloom of spring forage to support lactation and calf growth. Spring forage blooms on Antelope Island are predictable but short lived. Furthermore, minor blooms may occur at widely disparate times of the year, whenever sufficient moisture is available to produce germination of annual grasses. These conditions may produce some interannual variation in the timing of forage availability.

Green and Rothstein (1993) postulated lifelong negative effects to late-born bison calves, citing reduced growth and reproductive success, and negative effects on early dominance relationships as examples of birth-order effects. In addition, Berger (1989) further indicated that earlier calving cows were in better body condition and came into estrus earlier in the breeding season than later calving cows.

An interesting question is the apparent inconsistency that exists between the observed rate of decline in the mean annual pregnancy rate and the continued increase in population size (~7.0% per year). This herd of bison experiences little natural mortality, has no natural predators, and hunting is limited to the removal of 6–10 bulls per year. Culling practices do occur each year during the fall muster with the removal of approximately 10% of the animals from the herd for commercial purposes. To determine whether the number of reproductively mature females could continue to increase as it has over the last 10 yr, while experiencing a decline in annual pregnancy rate, we constructed a model to generate animal number estimates. Using assumptions of 90% survival rate and 50% female calf crop along with the actual annual pregnancy rates, we arrived at estimates of reproductively mature female herd size that were very close to actual numbers of animals in this group through 1994. Estimates generated for 1995 through 1997 were higher than actual numbers of mature females observed; nevertheless, growth in numerical size of this herd observed over the period 1988 through 1997 is not inconsistent with the observed rate of decline in mean annual pregnancy rate.

It is noteworthy that each year during the roundup some 15–20 red calves are encountered. These animals are generally reunited with their dams following processing. At a minimum these cows would not have been pregnant at that time, and the return of their calves could result in a delayed onset of estrus during the following breeding season.

In conclusion, the data presented here indicate that the management program implemented to increase reproductive performance in this herd has not been successful in accomplishing that objective. Elimination of winter/spring grazing by domestic livestock in 1987 may have temporarily reduced grazing pressure on the island's limited forage resources. In the interim, however, the increased size of the bison herd and active selection for larger body size have likely more than offset these gains and resulted in a higher level of year-round herbivory. Supplemental feeding of calves during a portion of their first year of life may help females achieve reproductive condition at an earlier age (i.e., 2 yr). However, it does not adequately compensate for the underlying poor forage condition on the island in order to sufficiently elevate the nutritional plane of females throughout their reproductive life. Large-scale range improvements are likely the only measure appropriate for this purpose.

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REMARKABLE WAXING, WANING, AND WANDERING OF POPULATIONS OF *MIMULUS GUTTATUS*: AN UNEXPECTED EXAMPLE OF GLOBAL WARMING

Robert K. Vickery, Jr.[1]

ABSTRACT.—The purpose of this study was to observe the dynamics of a meta-population of *Mimulus guttatus*. Changes in size and location of 16 original populations and the new populations established in their vicinities in Big Cottonwood Canyon, Salt Lake County, Utah, were observed for 25 yr. Twenty-three new populations appeared. Seven original populations and 13 new populations had become extinct by the end of the observation period in 1996. Many populations died out and were reestablished, often repeatedly, during the observation period. Altogether there were 54 population disappearances and 34 reappearances. Many populations changed size as much as 100-fold or more from year to year. There were spectacular examples of populations expanding to fill newly available, large habitats.

Frequent extinctions were due overwhelmingly to the canyon drying trend, which led to the drying up of most Mill D North drainage springs, creeks, and ponds. Precipitation and minimum temperatures increased moderately during the observation period. The growing season lengthened almost 50%, a typical consequence of global warming. The drying trend, lengthened growing season, and disappearance of *Mimulus* populations in Big Cottonwood Canyon appear to be a clear, local example of global warming.

Key words: Mimulus guttatus, *meta-population, global warming, growing season, colonization, recolonization, extinction, population fluctuations.*

Populations of *Mimulus guttatus* Fischer ex. D.C. in the upper reaches of Big Cottonwood Canyon form a *meta-population*, i.e., an interacting group of local populations (Van Der Meijden et al. 1992). This conclusion is based on my earlier study of gene exchange and selective pressures in these populations (Vickery 1978). The purpose of the present longitudinal study was to observe for a long enough period, 25 yr, the dynamics, that is, speed of turnover, of the local *M. guttatus* populations constituting the meta-population. How quickly and frequently do they increase or decrease in size, die out, colonize new habitats, or recolonize old ones? How do these changes relate to the environment—precipitation, insolation, temperature, and growing season?

STUDY SITES

For this research I studied a sample of 16 of the approximately 170 local populations of *M. guttatus* in the upper reaches (above the terminal moraine at 2150 m) of Big Cottonwood Canyon, Salt Lake County, Utah (Fig. 1). I observed the same set of populations studied in the selective pressure versus gene exchange study alluded to above (Vickery 1978). For that investigation I selected 4 side canyons of Big Cottonwood Canyon (Fig. 1, Table 1). Each side canyon or drainage is separated from the others by high ridges of up to 3000 m or more. Each contains a creek that runs from the side canyon headwaters at ca 2750 m down to its confluence with Big Cottonwood Creek at ±2250 m. I selected 4 study sites as equally spaced as possible along each of the creeks. Each study site contained 1 population of *M. guttatus*, the original study population (Table 1). Most study sites had 1 to 6 or more suitable habitats for local *M. guttatus* populations, although there was only the original study population at the beginning of the observation period.

Study sites for this moisture-loving species were in habitats by streams or springs, or along pond or lake shores. Some were in full sun but more were in partial shade of willows, small alders, or young aspen trees, while a few were in open areas or light gaps in the denser shade of the spruce forest. Habitats tended to be unstable and transitory. That is, the stream

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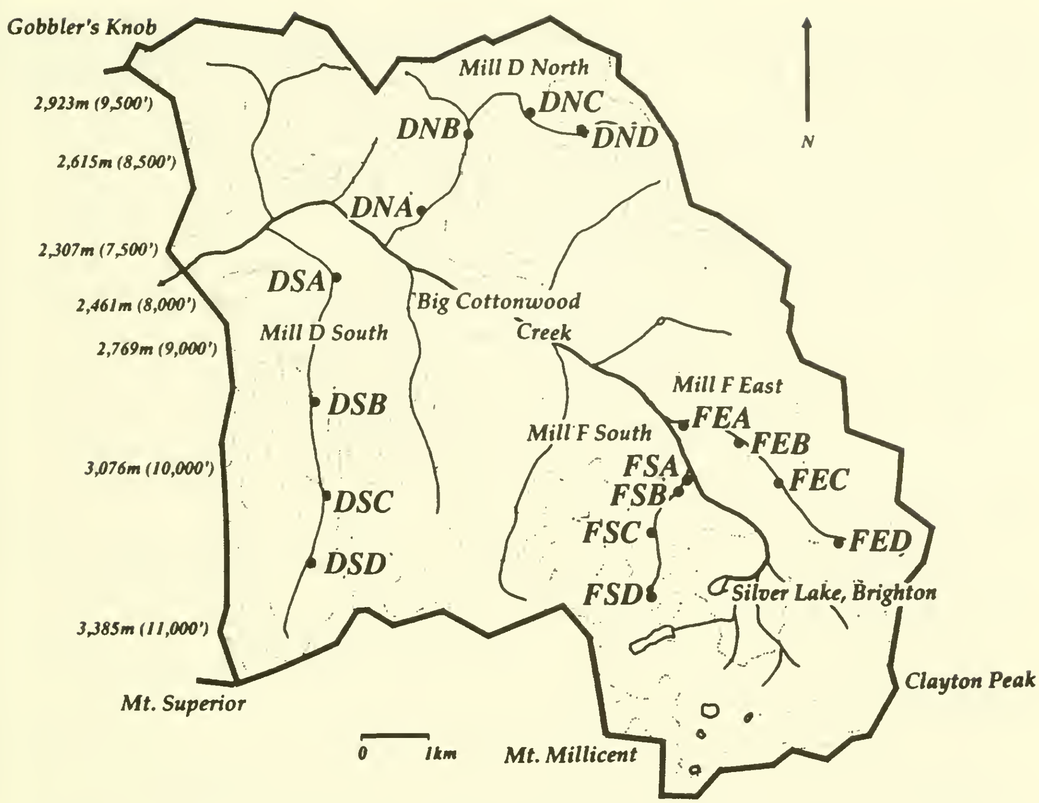
Gobbler's Knob
2,923m (9,500')
2,615m (8,500')
2,307m (7,500')
2,461m (8,000')
2,769m (9,000')
3,076m (10,000')
3,385m (11,000')
Mt. Superior
Mill D North
DNB
DNC
DND
DNA
N
DSA
Mill D South
Big Cottonwood Creek
DSB
DSC
DSD
Mill F East
FEA
FEB
FEC
FED
Mill F South
FSA
FSB
FSC
FSD
Silver Lake, Brighton
Clayton Peak
0
1km
Mt. Millicent

Fig. 1. Map of the upper reaches of Big Cottonwood Canyon in the Wasatch Mountains, Salt Lake County, Utah. Side canyons, drainages, and locations of study sites are indicated. (Based on maps of the area of the U.S. Geological Survey, Washington, DC 20242.)

would erode them, ponds or lakes would change level, and bushes and trees would grow, thus shading the populations; or, most importantly, streams would decrease or dry up, thereby killing the plants. Also, in some cases, deer or moose trampled the populations or pikas ate them.

M. guttatus local populations were separated one from another by spaces of several meters, often as much as 0.5 km, in which there were no *Mimulus* plants. These spaces typically were unsuitable for monkey flowers and were often filled with bushes, trees, and/or rocks.

MIMULUS GUTTATUS

Mimulus guttatus Fischer ex D.C. ranges from northern Mexico to the Aleutian Islands (type locality) and from the Pacific Coast to the Rocky Mountains; it has gone wild in Europe. A moisture-loving species that forms scattered, often isolated, local populations and only occasionally meta-populations, *M. guttatus* consists of at least 6 ecotypes (personal observation), including the Wasatch Mountains one to which the constellation of local populations of Big Cottonwood Canyon belongs. This ecotype is distinguished by its numerous rhizomes, but otherwise it is rather typical of the species. The species may be annual or rhizomatous perennial. Stems are erect, 2–60 cm high. Leaves are in opposite pairs, glabrous to pubescent, rounded-ovate, 1–10 cm long × 1–6 cm wide, with dentate margins. Lower leaves are petiolate, upper leaves sessile. Inflorescences are racemose, often few-flowered or solitary. On taller plants the flowers are mostly in pairs. Calyces are campanulate, 6–12 mm long, much inflated in maturity, the upper tooth longest. Corollas are 1–2 cm long, the throats spotted with red and the palate ridges hairy. Upper lips of the corollas are reflexed and much shorter than the

TABLE 1. Locations of study sites (by elevation, latitude, and longitude) and characteristics of habitats within the study sites of the original and new populations by location relative to the original population; area; insolation; average maximum and minimum temperatures for the 50-d heart of the season, 4 July–23 August 1973 (for the original populations); soil type; and source of moisture.

MILL D NORTH DRAINAGE—southwest facing

- **DNA study site,** elev. 2350 m, 40°38′57″N, 111°38′9″W
  - DNA, original population, 0.5 m², partial shade, 18.0°/5.3°, sandy gravel, streamside
  - DNA′, new population, 8 m down and across stream, 1.0 m², full sun, sandy gravel, streamside
- **DNB study site,** elev. 2520 m, 40°39′43″N, 111°37′40″W
  - DNB, original population, 30 m², full sun, 13.3°/2.6°, moss and gravelly soil, by large spring
- **DNC study site,** elev. 2670 m, 40°39′40″N, 111°37′4″W
  - DNC, original population, 2 m², partial shade, 15.3°/4.3°, grassy soil, by beaver pond
  - DNC′, new population, 20 m downstream, ca 350 m², deep loam, moist pond bottom
  - DNC″, new population, 40 m downstream, ca 150 m², deep loam, moist pond bottom
- **DND study site,** elev. 2760 m, 40°39′35″N, 111°36′38″W
  - DND, original population, 2.5 m², open shade of aspen, 14.3°/4.0°, sandy gravel, along a rill
  - DND′, new population, 30 m downstream, 6 m², sandy gravel, stream delta

MILL D SOUTH DRAINAGE (CARDIFF CANYON)—northeast facing

- **DSA study site,** elev. 2277 m, 40°38′27″N, 111°39′1″W
  - DSA, original population, 1.5 m², light gap in dense shade, 19.2°/6.8°, sandy, gravelly soil, streamside
  - DSA′, new population, 100 m upstream, ca 24 m², light gap in dense shade, loamy soil, boggy spring by stream
- **DSB study site,** elev. 2474 m, 40°37′34″N, 111°39′14″W
  - DSB, original population, 12 m², full sun, 14.3°/4.1°, moss, gravel, and pebbles, streamside
  - DSB′, new population, 3 m across stream, 14 m², full sun, moss, gravelly soil, streamside
  - DSB″, new population, 10 m downstream, 1 m², partial shade, sandy soil, streamside
- **DSC study site,** elev. 2628 m, 40°37′1″N, 111°39′14″W
  - DSC, original population, 2 m², partial shade, 18.8°/4.2°, loamy soil, by stream
  - DSC′, new population, 8 m downstream, 0.1 m², partial shade, loamy soil, by stream
- **DSD study site,** elev. 2763 m, 40°36′25″N, 111°39′19″W
  - DSD, original population, 18 m², full sun, shade at edges, 14.1°/4.5°, deep loam, in boggy spring
  - DSD′, new population, 20 m upstream, 3 m², partial shade, loamy soil, by small rill
  - DSD″, new population, 15 m downstream, 3 m², full sun, gravelly soil, by small rill

spreading lower ones. Capsules are oblong. Seeds are football shaped, ca 0.5 mm wide × 1.0 mm long and longitudinally striate. For fuller descriptions see Grant's monograph (Grant 1924) or the treatment in the Jepson manual (Thompson 1993).

Flowers, which are pollinated by bumble bees and occasionally by other insects, produce numerous seeds—50 to 250—per capsule. Reproduction is from seeds, but in this ecotype it is commonly from underground rhizomes as well.

M. guttatus plants of the canyon vary morphologically both within and among populations (see voucher specimens in the Garrett Herbarium [UT], University of Utah). Canyon plants range in height from 1 cm to 30 cm, in leaf length from 1 cm to 5 cm, and in number of flowers from none to a dozen or more. Differences among plants apparently are plastic responses to the varied environments of the canyon much as I showed for clone members of plants of one canyon population in the phytotron at Cal Tech (Vickery 1974). This plasticity was confirmed twice by growing sets of the 16 original study populations in uniform greenhouse environments. For the earlier set (Vickery 1978) plants were scored for over 100 traits and compared statistically. There were no significant differences. For the more recent set (Appendix A), plants were scored for a different, smaller set of traits and compared visually. There were no apparent differences.

METHODS

I counted or estimated the number of plants in each of the original study populations each year beginning in 1972 and concluding in 1996. Actual counts were made for small populations. Estimates, made for medium-sized and large populations, were based on counting 50 or 100 plants in an area and then multiplying by the number of such areas in the population

TABLE 1. Continued.

MILL F EAST DRAINAGE (GUARDSMAN PASS)—west facing
FEA study site, elev. 2524 m, 40°37′24″N, 111°35′25″W
FEA, original population, 24 m^2, deep shade, 13.5°/6.0°, moss and sand bars, in and beside stream
FEA′, new population, 100 m downstream, 1 m^2, full sun, gravelly soil, streamside
FEB study site, elev. 2615 m, 40°37′20″N, 111°35′3″W
FEB, original population, 2 m^2, open shade, 16.9°/3.1°, grassy soil, streamside
FEB′, new population, 12 m downstream, 1 m^2, open shade, sand bar, in stream
FEB″, new population, 3 m across stream, 5 m^2, open shade, loamy bank, edge of stream
FEB‴, new population, 5 m downstream, 1.5 m^2, open shade, sand bar, in stream
FEC study site, elev. 2670 m, 40°36′56″N, 111°37′33″W
FEC, original population, 6 m^2, partial shade, 14.4°/3.9°, loamy soil, by stream
FEC′, new population, 10 m upstream, 16 m^2, open shade, sand bar, in stream
FEC″, new population, 30 m upstream, 24 m^2, sunny, grassy loam, by stream
FEC‴, new population, 7 m upstream, 10 m^2, sunny, grassy loam, by stream
FED study site, elev. 2830 m, 40°36′34″N, 111°33′39″W
FED, original population, 0.5 m^2, partial shade, 16.6°/5.1°, gravelly loam, streamside
FED′, new population, 5 m upstream, 15 m^2, sunny, loamy soil, by stream
FED″, new population, 15 m downstream, 1 m^2, sunny, sandy gravel, streamside
MILL F SOUTH DRAINAGE (SOLITUDE CANYON)—northeast facing
FSA study site, elev. 2528 m, 40°37′4″N, 111°35′30″W
FSA, original population, 2 m^2, sunny, 13.5°/6.0°, grassy soil, streamside
FSA′, new population, 5 m upstream, 8 m^2, full sun, loamy soil and gravel, streamside and in stream
FSB study site, elev. 2560 m, 40°37′0″ N, 111°35′40″W
FSB, original population, 15 m^2, open shade, 17.6°/5.3°, sandy soil, streamside
FSB′, new population, 20 m south along new channel, 12 m^2, full sun, pockets of sandy soil amongst cobbles, in stream
FSC study site, elev. 2708 m, 40°36′47″N, 111°35′51″W
FSC, original population, 8 m^2, sunny, 13.2°/3.6°, loamy soil, by small spring
FSC′, new population, 20 m downstream, ca 600 m^2, full sun, in new grassy, loamy meadow, near stream
FSD study site, elev. 2770 m, 40°36′29″N, 111°40′56″W
FSD, original population, 10 m^2, sunny, 13.6°/3.7°, deep loam, edge of Lake Solitude
FSD′, new population, 25 m north along lake shore, 12 m^2, sunny, deep loam, lake shore
FSD″, new population, 50 m west along lakeshore, ca 12,000 m^2, full sun, deep loam, exposed lake bottom

to obtain the estimated population size. Numbers were rounded off. A rosette was considered to be a plant. In some cases I found that 2 or 3 rosettes were connected by underground stems. Stems would decay as the season progressed so that rosettes became independent plants, although some would share the same genotype, as observed by Waser et al. (1982) for other populations of *Mimulus guttatus*. Population counts were made in late summer or early fall as populations were at their maximum toward the end of the growing season. Random duplicate counts were made to check the accuracy of counts and estimates. They varied by 10% to 20%, which is modest considering the very large differences noted among different local populations the same year or among different years of the same population. The vicinity of each population was checked to see if new populations had become established. If they had, their locations were noted and they too were scored as above.

Air temperature of each study site in 1973 (Table 1) was measured using Temp Scribe recorders (Vickery 1978). Temperature, precipitation, snowpack, and growing season data for the entire 25-yr observation period were obtained from U.S. Climatological Data for Utah (Environmental Data Services 1972–1996) for Silver Lake (40°33′48″N, 111°35′4″W), at the head of Big Cottonwood Canyon (Fig. 1).

RESULTS

Populations ranged widely in size from a single plant to 37,000 plants (Appendix B). Some populations did not vary in size from year to year while others waxed or waned with time. Still others varied dramatically over the period of a few years (Figs. 2–5).

Of the 16 original study populations, 7 had disappeared by the end of the 25-yr observation period (Appendix B). Not only were they gone, but each one had disappeared and reappeared

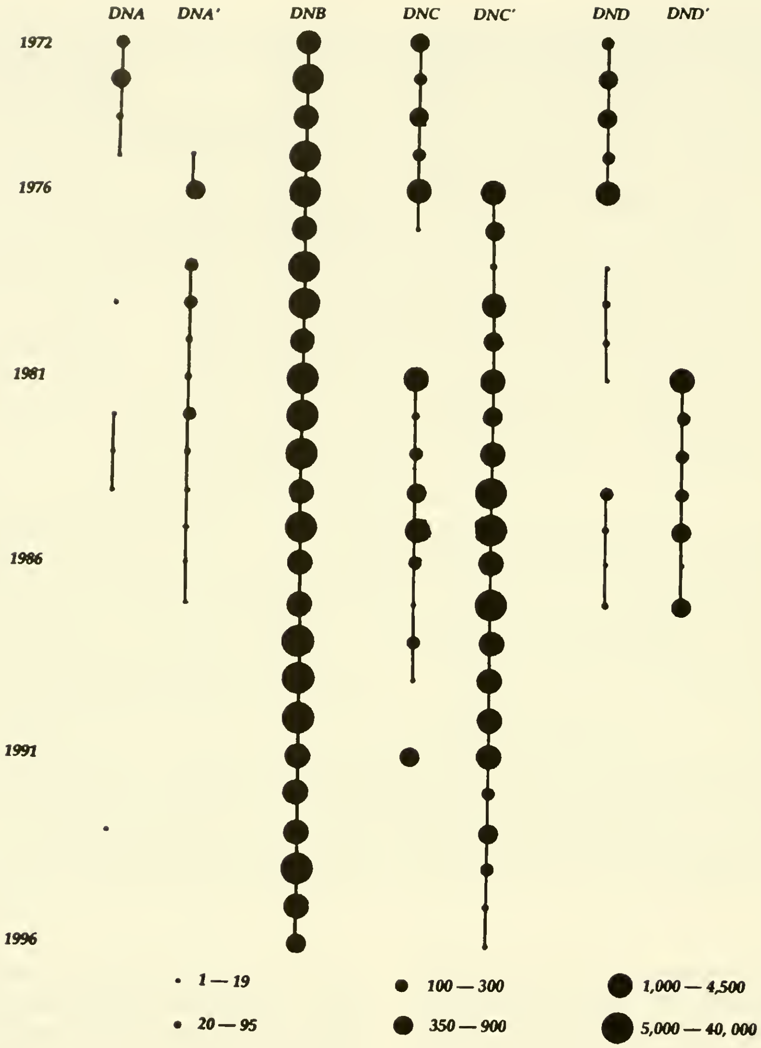

Fig. 2. Mill D North drainage. Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

at least once prior to its final disappearance. Of the 9 original populations still present at the end of the observation period, 4 had disappeared and reappeared. Only 5 of the original populations had been present throughout the study (Figs. 2–5).

Twenty-three new populations—almost 1 per year—appeared in study sites in the vicinity of the original populations (Figs. 2–5, Appendix B). They disappeared and reappeared like the original populations. At the end of the observation period only 10 new populations were still present and only 4 had been consistently present since they appeared.

The number of populations climbed from the original 16 to an average of 23 (Table 2). Once the higher value was attained, there was a dynamic equilibrium of populations appearing, disappearing, and reappearing. Numbers climbed as high as 30 and declined to as low as 15 (Table 2, Fig. 6). The establishment of populations depended on availability of suitable (moist, without too much shade or plant competition) habitats within each of the 16 study sites.

The disappearance of populations reflected loss of suitable habitats, the most common cause being loss of moisture. Drying could be

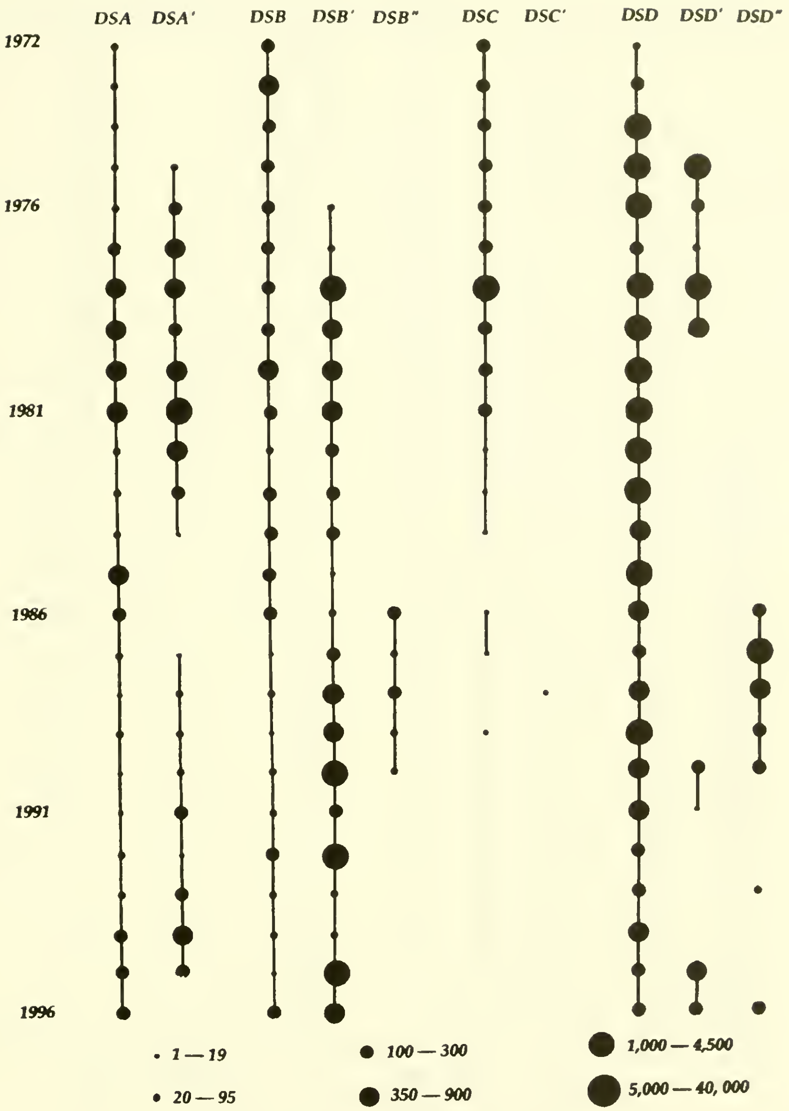

Fig. 3. Mill D South drainage (Cardiff Canyon). Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

transitory (i.e., short term—1–3 yr) or prolonged (i.e., long term—more than 3 yr). Altogether there were 54 cases of populations disappearing (Table 2). Twenty-six were due to short-term drying and 12 to long-term drying. In addition to drying out, 7 populations disappeared because erosion removed their habitats, another 4 were lost apparently due to competition, and 5 more to shading from a dense overstory (Table 2).

DISCUSSION

The most striking results of my observations were fourfold: (1) the remarkably large changes in population size from one local population to the next and from one year to the next for the same population; (2) the high frequency with which populations appeared, both new ones and old ones, after an absence; (3) the high rate at which both new and old

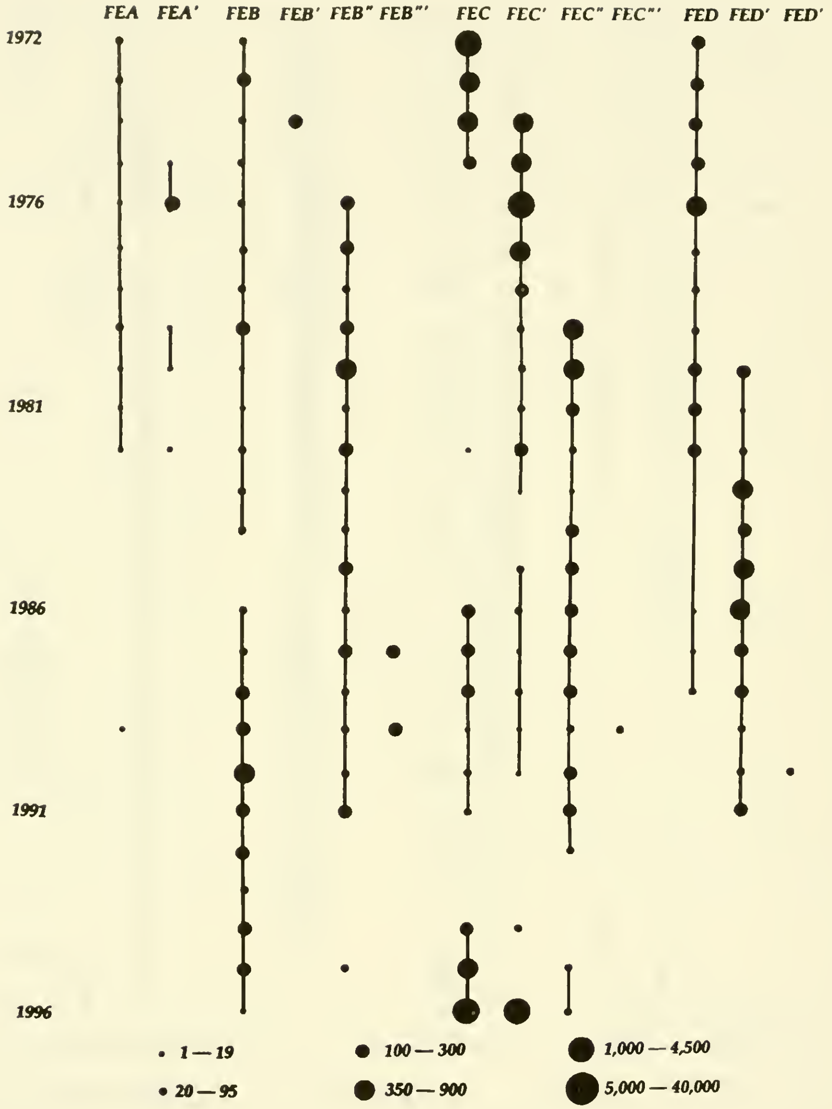

Fig. 4. Mill F East drainage. Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

populations disappeared; and (4) probably the most important, the implications of population disappearance for global warming.

Population Sizes

The size of a population reflects available habitat area, which in turn reflects soil type, plant competition, and climatic parameters of insolation, precipitation, and temperature. Soil type did not appear to be limiting inasmuch as *M. guttatus* grew on all substrate types, from sand bars to loamy bogs. Competition could be limiting (e.g., dense meadow grasses), but usually it was not a determining factor. Insolation, the amount of sunlight, rarely was limiting except in the case of deep shade. Precipitation, rain and snow, at the actual habitat was irrelevant because this moisture-loving species required habitats to begin with that were steadily moist, e.g., stream banks. However, precipitation for the canyon as a whole was relevant for recharging the aquifers that supplied the springs and streams. Very wet years appeared to enhance competition at the expense

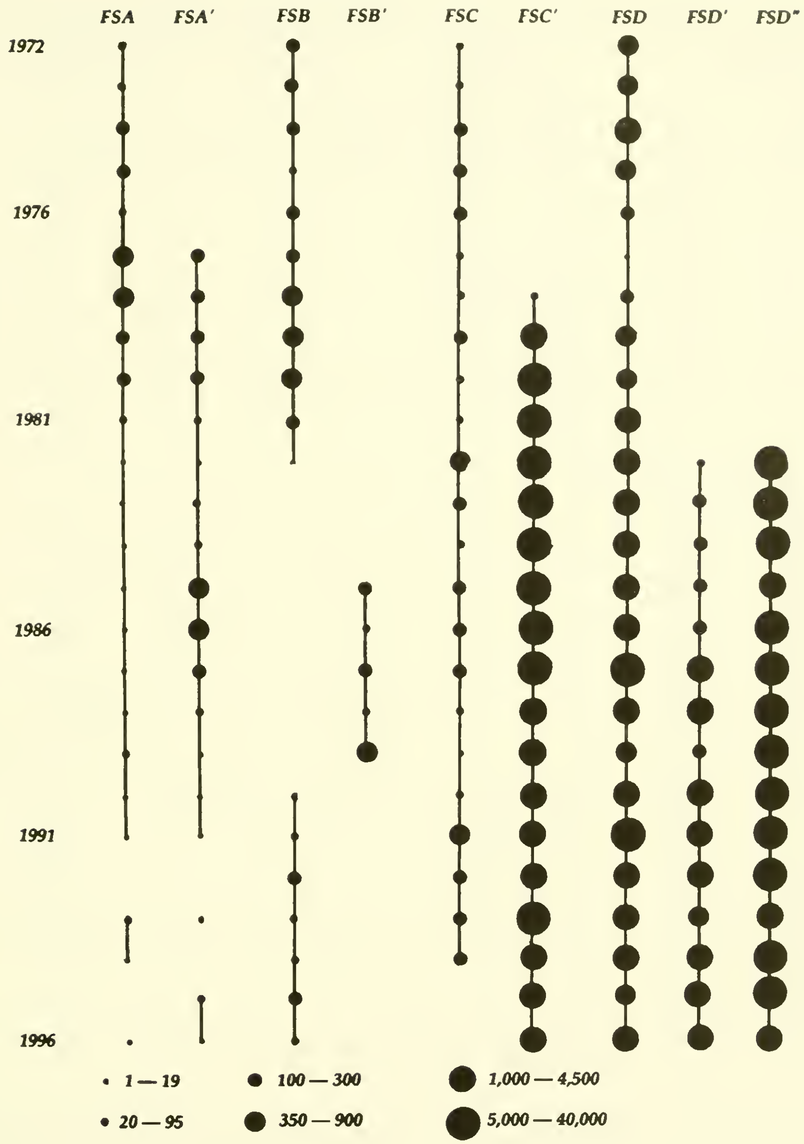

Fig. 5. Mill F south drainage (Solitude Canyon). Representation of changing sizes of the original study populations and new populations over 25 yr of observation.

of *M. guttatus* population size. Temperature of the actual habitat was relatively unimportant, as *Mimulus guttatus* has a wide norm of reaction for temperature (Vickery 1974). However, for the area as a whole, temperature was important, particularly because it shortened or lengthened the growing season (Myneni et al. 1997). Warmer temperatures did appear to lead to larger *Mimulus* populations, as seen, for example, in comparing population sizes in 1994 (the hottest year of the study) with those in 1993 (the coldest year of the study; see Appendix B).

Population sizes could be roughly grouped into 3 categories. Small populations (1 to 20) were usually part of a sequence in the process of population decline toward extinction. In many cases these populations would grow smaller and smaller, disappear, reappear, and finally disappear for the remaining observation period.

TABLE 2. Population appearances, disappearances, numbers and parameters of the environment from U.S. Weather

	Appearances		Disappearances				
Year	# new populations	# recolonized	Drying—short term	Drying—long term	Competition	Shading	Erosion
1972	—	—	—	—	—	—	—
1973	0	0	—	—	—	—	—
1974	2	0	—	—	—	—	—
1975	4	0	—	—	—	—	FEB′
1976	3	0	DNA	—	—	—	FEC
1977	1	0	DNA, DND, FEA	—	—	—	
1978	1	2	—	—	DNC	—	—
1979	1	2	—	—	—	—	—
1980	1	0	DNA	DSD′	—	—	—
Totals (1972–1980)	13	4	5	1	1	0	2
1981	1	1	FEA′	—	—	—	—
1982	2	3	DND	—	—	—	—
1983	0	0	FEC	FEA, FEA′	—	FED	FSB
1984	0	1	FEC′	—	—	—	—
1985	1	1	DSA′	DNA	FEB	DSC	—
1986	2	4	—	—	—	—	—
1987	1	1	—	—	—	—	—
1988	1	0	—	DNA′, DND, DND′	—	DSC	FEB‴
1989	1	3	—	FED	—	DSC′	—
1990	1	2	—	FEA	DNC	DSC	FEB‴, FEC‴, FSB′
1991	0	1	DSD″, FEC′	DSB″, FED″	—	—	—
1992	0	0	FEB″, FEC, FSA, FSA′, DSD′	FED′	DNC	—	—
1993	0	4	FEC′	—	—	—	—
1994	0	2	DNA, FSA′, DSD″	—	—	—	—
1995	0	4	FSA, FSC, FEC′	—	—	—	—
1996	0	3	FEB″, DSA′	—	—	—	—
Totals (1981–1996)	10	30	21	11	3	5	5
Totals (1972–1996)	23	34	26	12	4	5	7

Medium-sized populations (20 to 900) usually reflected stable habitats. Sizes of these populations were limited by the carrying capacity of their habitats and often fluctuated around a value well below the observed maximum number of plants. Large populations (1000 or more) grew in large, favorable habitats.

The close relationship between population size and habitat area was vividly demonstrated in several cases. For example, Solitude Ski Resort bulldozed a large (30 m × 50-m) thicket of willows at the FSC study site. This not only improved the ski run but opened a large, sunny, moist meadow with little plant competition. *Mimulus* immediately invaded via seeds from FSC and upstream populations. Where there had been no *Mimulus* in 1978, in 5 yr time there were 37,000 plants in this new, large, excellent habitat (Fig. 5, Appendix B). In time the original FSC population declined as its spring source wandered off. Another example of a population explosion occurred at the DNC study site. The adjacent beaver pond dried up in 1977, exposing a large (30 m × 40-m)

Service records for Silver Lake, Big Cottonwood Canyon, Utah.

Total # populations	July–August avg. temperatures		July–Aug. precip. (mm)	Winter season (< –2.2°C)		Growing season		
	Max. (°C)	Min. (°C)		Total precip. (mm)	Snowpack (m)	Start	End	Number of days
16	22.6	5.3	27	1123	11.5	—	9/12	—
16	20.8	5.5	104	1131	13.4	6/5	—	—
18	21.8	5.3	64	1073	13.6	6/9	7/13	23
21	21.1	5.3	31	1258	12.2	6/26	8/28	62
22	22.1	6.2	32	434	7.0	6/26	8/28	62
20	21.1	6.2	136	669	5.1	5/30	9/18	110
22	21.4	5.2	63	1246	11.7	6/16	8/17	61
25	21.3	5.8	72	950	10.0	6/9	9/14	96
24	22.0	6.4	47	1162	12.6	6/16	8/20	64
$\bar{x}$ = 20	21.6	5.7	64	1005	10.8	6/14	8/24	68
25	22.7	7.6	55	905	7.0	6/15	9/26	102
29	21.2	6.6	127	1422	13.9	6/9	9/12	94
24	—	—	—	1500	13.8	6/14	9/20	97
24	20.9	6.4	132	1529	14.1	6/11	9/22	102
22	22.5	6.1	66	1294	12.5	5/30	9/13	105
28	21.1	6.9	140	1401	11.8	5/23	9/16	115
30	19.9	5.6	155	968	7.5	5/26	9/17	113
26	23.2	7.4	18	794	6.7	5/31	9/11	102
28	21.8	7.6	94	1021	10.2	6/22	8/25	63
25	21.6	7.0	71	880	8.3	—	10/7	—
22	21.5	7.4	132	967	9.3	5/28	9/15	109
15	21.1	6.4	137	847	7.0	5/10	8/26	107
18	19.3	4.3	131	1345	12.7	6/24	8/30	66
17	23.8	8.1	99	—	—	6/21	10/7	138
18	21.6	6.6	57	—	—	6/22	9/22	91
19	23.2	7.6	47	—	—	5/31	9/17	108
$\bar{x}$ = 23	21.7	6.8	97	1144	10.4	6/5	9/14	101
$\bar{x}$ = 22	21.7	6.4	85	1087	10.5	6/10	9/8	90

expanse of moist pond bottom into which *Mimulus* seeds invaded from the DNC population. The new DNC′ population steadily increased for a decade from 0 to well over 8000 plants (Fig. 2, Appendix B).

Populations Appearing

Populations appeared and reappeared in suitable, moist habitats along stream banks, by ponds, along lake shores, and by or in tributary springs. Such habitats were colonized in all 16 study sites near the original study populations except in DNB with its large ($\bar{x}$ < 6500) original study population that effectively filled all suitable habitats in the vicinity of its large spring.

Populations are easily established or reestablished from seeds floating downstream from upstream plants that often overhang the stream and shed their seeds into the water (Lindsay and Vickery 1964, Waser et al. 1982). Also, populations may be established by windblown seeds (Vickery et al. 1986). Windblown seeds rarely travel more than 5 m, whereas

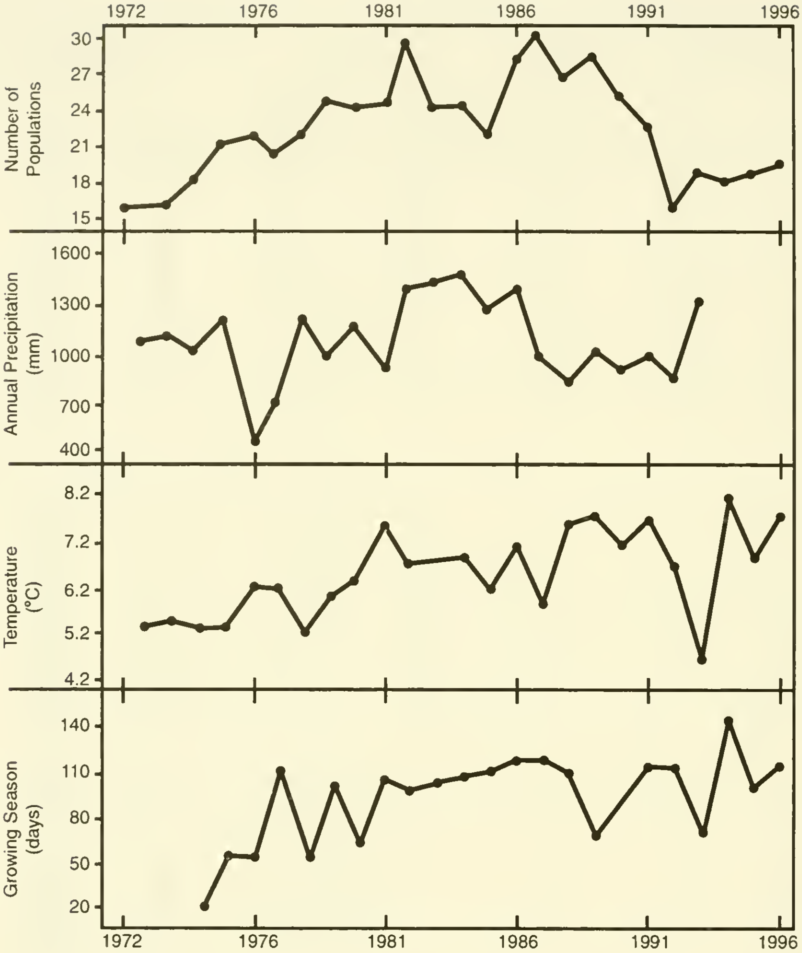

Fig. 6. Plot of population number, annual precipitation, minimum average temperatures for July–August, and length of growing season against years. The growing season is the period between the last spring minimum temperature of −2.2°C (28°F) and the first fall minimum of −2.2°C (28°F).

water-borne seeds can travel for hundreds of meters.

The actual source of the "rain" of floating seeds for population establishment or reestablishment could be identified in a few cases. For example, for the new DSD′ population the seed source must have been the original study population, DSD, because there were no other upstream populations. Windblown seeds can be inferred as the source for some populations, e.g., for the new FED′ population where seeds must have come from the only nearby, but downstream, population, FED.

Mimulus guttatus populations that reappear in 1, 2, or even 3 yr at the same site probably do so from dormant rhizomes or more likely from seeds in the seed bank at that site (Thompson 1987, Leck et al. 1989). Occasionally, I have observed dormant rhizomes under rocks. *Mimulus guttatus* seed bank seeds can readily survive for 2 or 3 yr, but not in large quantities (Vickery unpublished study).

Populations Disappearing

Disappearances of populations, both original study populations and newly established ones, were due to habitats becoming too shady or too crowded with competitors, or to their being eroded away by the stream or trampled by animals. However, the disappearance of populations was due overwhelmingly to habitat drying (Table 2).

The disappearance of several populations was caused by shading of habitats. For example, FEA was shaded out by an increasingly dense stand of spruce trees. The DSC population was first partially eaten, then trampled, and finally shaded out by the growth of willow thickets. The pattern of decline due to shading was a gradual decrease in population size accompanied by a decrease in plant size and amount of flowering, finally resulting in no monkey flower plants. Increasing competition led to much the same pattern of decline. For example, DNC declined to extinction as meadow grasses of the site increased and formed a dense turf. The stream swept away some populations, particularly ones established on sand bars, such as FEB′ and FEB‴, much as Porath et al. (1987) observed for the fugitive species *Verbascum sinaiticum* on the gravel bars of wadis in the Negev Desert.

Canyon Drying Trend

Drying of population habitats was part of a pronounced drying trend in Big Cottonwood Canyon that began in the late 1970s and early 1980s—in 1981 on average. The drying trend strongly affected Mill D North and Mill F East drainages, both of which are southwest facing, meaning they have high insolation. Also, their aquifers are shallow (D. Scheck personal communication). The whole of the initially flowing Mill D North creek dried up except for the moist beaver pond bottom at DNC and the large spring and stream immediately below it at DNB (see Fig. 1). The 4 original populations had increased to 7 in the early 1980s, but as the drying trend set in, populations declined to just 2 by the early 1990s, and those 2 were rapidly waning by the end of the observation period (Appendix B). In the Mill F East drainage, the top spring and ca 100 m of stream below it dried up as well as the bottom ca 200 m of stream. The 4 initial populations had increased to 13 in the course of the observation period. By the end of the period 5 populations had dried out and disappeared—all 3 of the top and both bottom populations. Four intermediate level populations had disappeared due to erosion. The original FEB populations appeared to be on the way to extinction. However, 3 of the FEC site populations were flourishing. Altogether over 1/3 of the population had disappeared due to the drying trend.

Global Warming

What caused the drying trend? Counterintuitively, decreased precipitation was not the cause (Fig. 6). Beginning in 1981, precipitation actually increased from an average of 1000 mm to an average of almost 1150 mm (Table 2). Insolation, presumably, remained constant. Increased temperature probably played a role. However, the July–August average maximum temperature was not higher, but the average minimum temperature was 1°C higher. These temperatures follow the same pattern noted by Karl in his global warming study of the arctic slope of Alaska, also beginning in 1981 (Waring and Running 1998). In Big Cottonwood Canyon, the growing season (Fig. 6) lengthened by almost 50%, from an average of 68 d (1971–1980) to an average of 101 d (1981–1996; see Table 2). Lengthening of the growing season is the hallmark of global warming, according to a satellite study of the northern latitudes (Myneni et al. 1997). The drying trend in Big Cottonwood Canyon appears to be a specific, local example of global warming.

How does a lengthened growing season translate into the observed drying trend? The immediate result of a longer season is increased evapotranspiration from the aspen forest and its understory of shrubs, herbs, and grasses (J. Ehleringer personal communication). The consequence of increased evapotranspiration is the drying out of surface soil, which may lead to a failure to recharge underlying aquifers, which are shallow anyway (D. Sheck personal communication). Depletion of the aquifers results in springs drying up which, in turn, leads to streams and ponds drying up. Since there is considerable normal variability in precipitation, temperature, and length of growing season and hence of spring and stream flows, *Mimulus* populations often dry out and die only to be briefly reestablished as the drying trend proceeds. The drying out and disappearance of so many local populations of the extensive meta-population of *M. guttatus* in Big Cottonwood Canyon was due to the pronounced canyon drying trend, the root cause of which appears to be global warming.

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APPENDIX A. Characteristics of the 16 original study populations when grown under standard conditions in the Biology Department greenhouse, University of Utah[a].

Population[b]	Plant height (cm)	Days to flowering	No. of flowers	Dry wt. stems (g)	Dry wt. runners (g)	Largest leaf at 1st flower (cm)		Healthy typical flower (cm)	
						Length	Width	Length	Width
DSA	24	69	9	2.4	5.9	6.1	4.3	4.1	2.5
DSB	30	86	15	1.1	3.2	7.7	3.1	3.1	2.5
DSC	26	69	24	3.1	1.4	6.8	4.8	2.9	2.6
DSD	—[c]	—	—	—	—	—	—	—	—
DNA	38	67	21	1.5	4.6	7.8	4.9	2.8	2.5
DNB	49	52	38	2.6	2.4	5.2	3.9	2.3	1.9
DNC	34	44	21	0.7	1.4	4.7	3.4	2.2	2.4
DND	33	56	20	1.2	1.5	5.6	4.4	2.4	1.9
FSA	—	65	—	—	—	5.6	3.7	2.4	2.2
FSB	30	62	20	2.3	4.6	5.6	4.4	2.7	2.3
FSC	—	—	—	—	—	—	—	—	—
FSD	—	50	—	—	—	6.6	6.3	2.6	2.3
FEA	35	59	35	2.9	3.5	9.0	5.3	2.9	2.5
FEB	40	65	63	2.4	1.8	7.2	4.1	2.6	2.1
FEC	30	74	20	1.8	6.4	5.9	3.7	2.8	2.5
FED	—	62	—	—	—	9.3	4.5	2.6	2.4
$\bar{x}$	34	63	26	2.0	33	6.6	4.3	2.7	2.3

[a] Based on the means of 5 plants

[b] See Table 1 for population site data.

[c] Virus killed plants

APPENDIX B. Sites and sizes of original and new populations. Site abbreviations are described in Table 1.

Year	DNA	DNA′	DNB	DNC	DNC′	DND	DND′
MILL D NORTH DRAINAGE							
1972	100	—	2,000	500	—	200	—
1973	700	—	5,000	200	—	550	—
1974	30	—	2,500	350	—	400	—
1975	2	1	6,000	250	—	300	—
1976	0	450	20,000	1,250	2,000	1,500	
1977	0	0	1,000	12	200	0	—
1978	0	100	10,000	0	50	1	—
1979	1	150	7,000	0	1,500	35	—
1980	0	50	3,000	0	600	60	—
1981	0	35	8,500	1,100	1,700	6	1,000
1982	4	146	27,800	50	350	0	260
1983	3	36	19,000	200	1,500	0	100
1984	7	7	3,500	350	8,500	100	150
1985	0	8	6,000	1,200	8,000	25	500
1986	0	10	2,900	200	3,000	1	5
1987	0	6	1,000	2	6,000	40	800
1988	0	0	5,000	250	4,100	0	0
1989	0	0	12,000	10	3,000	0	0
1990	0	0	5,000	0	2,000	0	0
1991	0	0	3,000	500	4,000	0	0
1992	0	0	2,400	0	300	0	0
1993	8	0	2,500	0	600	0	0
1994	0	0	9,000	0	250	0	0
1995	0	0	1,500	0	50	0	0
1996	0	0	120	0	15	0	0

Year	DSA	DSA′	DSB	DSB′	DSB″	DSC	DSC′	DSD	DSD′	DSD″
MILL D SOUTH DRAINAGE										
1972	20	—	100	—	—	100	—	30	—	—
1973	60	—	500	—	—	300	—	200	—	—
1974	55	—	176	—	—	200	—	1,100	—	—
1975	45	50	200	—	—	150	—	2,400	1,050	—
1976	50	100	200	50	—	150	—	3,000	100	—
1977	100	400	150	30	—	280	—	250	50	—
1978	850	350	300	1,000	—	2,700	—	2,200	4,400	—
1979	600	300	250	800	—	200	—	3,000	400	—
1980	700	620	600	700	—	100	—	3,000	0	—
1981	600	1,000	100	600	—	100	—	2,000	0	—
1982	81	700	95	265	—	16	—	1,015	0	—
1983	23	250	250	230	—	4	—	1,250	0	—
1984	55	12	110	200	—	5	—	475	0	—
1985	400	0	300	5	—	0	—	1,200	0	—
1986	200	0	100	25	150	6	—	900	0	300
1987	60	12	6	120	50	4	—	235	0	1,000
1988	12	40	30	400	300	0	15	750	0	600
1989	60	30	6	850	50	1	0	1,000	0	100
1990	3	80	40	1,200	40	0	0	650	200	150
1991	3	250	50	100	0	0	0	400	15	0
1992	35	5	100	1,600	0	0	0	300	0	0
1993	24	150	30	50	0	0	0	200	0	50
1994	130	350	24	75	0	0	0	575	0	0
1995	120	200	12	1,000	0	0	0	200	750	0
1996	250	0	100	500	0	0	0	100	150	100

APPENDIX B. Continued.

Year	FEA	FEA′	FEB	FEB′	FEB″	FEB‴	FEC	FEC′	FEC″	FEC‴	FED	FED′	FED″
MILL F EAST DRAINAGE													
1972	70	—	25	—	—	—	1,500	—	—	—	120	—	—
1973	24	—	150	—	—	—	500	—	—	—	200	—	—
1974	6	—	30	100	—	—	500	500	—	—	300	—	—
1975	11	5	50	0	—	—	200	600	—	—	100	—	—
1976	12	100	50	0	100	—	0	1,500	—	—	600	—	—
1977	6	0	75	0	300	—	0	500	—	—	75	—	—
1978	15	0	30	0	70	—	0	150	—	—	70	—	—
1979	25	5	150	0	220	—	0	60	450	—	50	—	—
1980	10	6	8	0	450	—	0	20	500	—	200	200	—
1981	12	0	18	0	40	—	0	20	135	—	150	10	—
1982	3	5	36	0	220	—	3	120	70	—	110	30	—
1983	0	0	50	0	50	—	0	4	6	—	0	500	—
1984	0	0	20	0	95	—	0	0	100	—	0	160	—
1985	0	0	0	0	105	—	0	35	100	—	0	450	—
1986	0	0	20	0	30	—	100	40	100	—	5	800	—
1987	0	0	30	0	150	250	200	3	200	—	10	300	—
1988	0	0	120	0	25	0	140	60	200	—	40	250	—
1989	4	0	175	0	30	120	10	10	55	25	0	24	—
1990	0	0	475	0	20	0	30	1	100	0	0	50	50
1991	0	0	150	0	150	0	50	0	150	0	0	200	0
1992	0	0	250	0	0	0	0	0	80	0	0	0	0
1993	0	0	50	0	0	0	0	0	0	0	0	0	0
1994	0	0	150	0	0	0	150	20	0	0	0	0	0
1995	0	0	200	0	50	0	600	0	40	0	0	0	0
1996	0	0	15	0	0	0	1,000	1,000	50	0	0	0	0

Year	FSA	FSA′	FSB	FSB′	FSC	FSC′	FSD	FSD′	FSD″
MILL F SOUTH DRAINAGE									
1972	50	—	100	—	30	—	500	—	—
1973	60	—	150	—	50	—	450	—	—
1974	120	—	220	—	150	—	1,000	—	—
1975	240	—	40	—	150	—	600	—	—
1976	20	—	100	—	200	—	300	—	—
1977	350	150	100	—	20	—	2	—	—
1978	500	250	600	—	30	50	150	—	—
1979	250	200	400	—	100	2,000	600	—	—
1980	250	200	600	—	60	20,000	600	—	—
1981	20	30	100	—	50	21,500	4,000	—	—
1982	2	5	1	—	500	37,000	1,500	50	7,500
1983	1	20	0	—	150	10,000	1,250	100	12,650
1984	2	30	0	—	80	10,750	1,400	100	14,500
1985	3	350	0	255	150	9,000	1,200	100	3,500
1986	12	800	0	18	250	5,650	1,100	200	9,700
1987	2	100	0	150	120	26,700	7,000	1,200	20,000
1988	1	25	0	60	20	2,900	2,500	1,500	5,000
1989	30	12	0	350	2	1,000	800	200	12,000
1990	4	12	50	0	40	1,200	3,700	1,600	14,000
1991	3	5	70	0	450	2,400	6,000	1,500	8,800
1992	0	0	220	0	100	4,200	3,000	2,000	18,000
1993	20	1	60	0	200	6,500	1,000	500	4,000
1994	8	0	30	0	100	4,300	3,000	2,000	11,000
1995	0	40	175	0	0	2,950	750	3,000	5,000
1996	1	11	60	0	0	3,850	1,500	2,300	3,500

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BIOGEOGRAPHY AND PHYSIOLOGICAL ADAPTATIONS OF THE BRINE FLY GENUS *EPHYDRA* (DIPTERA: EPHYDRIDAE) IN SALINE WATERS OF THE GREAT BASIN

David B. Herbst[1]

ABSTRACT.—Four species of the genus *Ephydra* are commonly found in saline waters within the hydrologic Great Basin: *E. hians*, *E. gracilis*, *E. packardi*, and *E. auripes*. Though none of these brine flies is endemic (distributions also occur outside the Great Basin), they all inhabit distinctive habitat types and form the characteristic benthic insect fauna of inland saline-water habitats. The affinities of each species for different salinity levels and chemical compositions, and ephemeral to perennial habitats, appear to form the basis for biogeographic distribution patterns. Within any habitat, changing salinity conditions over time may impose physiological or ecological constraints and further alter patterns of population productivity and the relative abundance of co-inhabiting species.

Based on the physiology of salt tolerance known for these species, high salinity conditions favor *E. hians* in alkaline water and *E. gracilis* in chloride water. At lower salinities, based on limited habitat data, *E. auripes* and *E. packardi* are often more common, again showing respective preferences for alkaline and chloride chemical conditions. Specialized adaptations for alkaline carbonate waters are found in the larval Malpighian tubule lime gland of the alkali fly *E. hians*, while high salt tolerance in *E. gracilis* appears to be conferred by high hemolymph osmolality. Adaptation to ephemeral and low salinity conditions may be accomplished by swift adult colonizing ability and rapid larval development rates.

It is hypothesized that adaptive specializations in both physiology and life history and varied geochemistry of saline water habitats across the Great Basin produce the biogeographic pattern of distributions for species in this genus. This perspective on the genus *Ephydra*, and possibly other biota of mineral-rich Great Basin waters, suggests that interconnections among pluvial lakes may be less relevant to aquatic biogeography than chemical profiles developing in remnant lakes and ponds with the progression of arid post-pluvial climatic conditions.

Key words: Ephydra, *saline lakes, Great Basin, osmoregulation, biogeography, salt tolerance.*

Ever since the studies of Hubbs and Miller (1948), biogeographic studies of the aquatic fauna of the Great Basin have been dominated by a search for vicariance patterns. Distributions of fish species often revealed patterns suggesting pluvial interconnections among lake basins and provided evidence for post-pluvial hydrographic changes including isolation leading to extinctions and species differentiation (Miller 1946, Smith 1978). In addition to fish, other obligate aquatic species (e.g., spring snails, leeches, molluscs) have received an inordinate amount of attention because of the potential for endemic distributions arising out of the vicariance events of pluvial lake drying and recession, and the example set by Hubbs and Miller (Taylor 1960, Hershler 1989, Hovingh 1995). Insects with poor dispersal ability have also been studied in some depth in the Great Basin (e.g., Naucoridae; Polhemus and Polhemus 1994), but biogeographic patterns for most other aquatic invertebrates within the Great Basin have been only incompletely described. Habitat affinities are poorly known, and collection records typically have no associated physical or chemical data.

In addition to geographic barriers, differentiation of populations may also result from differences in the physical and chemical features of aquatic habitats without producing geographic isolation and endemism. Selection for physiological adaptation may restrict species distributions to certain habitat types. Great Basin aquatic habitats often include waters with varied chemistry derived from high mineral content. The closed-basin drainages that define the Great Basin collect and evaporate water in saline lakes, ponds, and wetlands. Many springs (geothermal and otherwise) contain high concentrations of dissolved solutes and trace minerals. Streams in lower elevations of the basin and range also typically have relatively high conductivity and alkalinity. Physical conditions also may be quite varied in terms of thermal regime (hot springs) and ephemeral and episodic filling of playas and intermittent streams. Gradients of chemical and physical variation form a habitat template that sets the stage for adaptive syndromes determining the distribution and abundance of species (*sensu* Southwood 1977).

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Geochemical evolution of major solutes in closed-basin saline lakes (e.g., Eugster and Jones 1979) may be a useful model for following progression and patterns in the biological evolution and distribution of saline water biota throughout the Great Basin. Water chemistry is determined primarily by the following factors:

- drainage basin lithology of inflowing waters (especially igneous vs. sedimentary);
- mineral precipitation pathways depending on the initial ratio of bicarbonate to calcium and magnesium and resulting in lake brines with differing contents of the major cations $Na^+/Ca^{+2}/Mg^{+2}$ and major anions $Cl^-/SO_4^{-2}/CO_3^{-2}$ (high bicarbonate generally evolves into alkaline brines and low bicarbonate into chloride-sulfate brines, and low salinity conditions may retain similar content of bicarbonate and Ca/Mg without forming precipitates);
- fractionation processes which enrich highly soluble (conservative) ions such as Na and Cl and deplete others through carbonate mineral formation, release of carbon dioxide gas, and biogenic reduction of sulfate for example.

Progressive enrichment from carbonate to sulfatochloride to chloride waters appears to occur with the concentration of inflowing waters over time and distance along interconnected evaporation basins of varied volume (Hutchinson 1957). Spatial and temporal components of variation in water chemistry form a habitat template that may be the foundation for shaping the distribution of saline water organisms.

Four species of the genus *Ephydra* are commonly found in saline waters within the hydrologic Great Basin: *E. hians*, *E. gracilis*, *E. packardi*, and *E. auripes*. Though none of these brine flies is endemic (distributions also occur outside the Great Basin), they inhabit distinctive habitat types and form the characteristic benthic insect fauna of inland saline water habitats. Wirth (1971) first suggested that some *Ephydra* had particular chemical preferences. The objective of this paper is to present evidence for the hypothesis that affinities of each species for different salinity levels and chemical compositions, and ephemeral to perennial habitats, form the basis for biogeographic distribution patterns.

METHODS

Contrasts of physiological specializations for habitat chemistry are presented here as evidence of adaptations that determine biogeographic patterns. Data for comparisons of osmoregulatory physiology and salt tolerance in *Ephydra* were derived from published research (Nemenz 1960, Herbst et al. 1988). Calculations of relative costs of osmoregulation were determined by applying the known osmotic gradients to calculations of the relative energy required for the work of active transport. Data on the range of known development times in *Ephydra* were also summarized from published sources (Ping 1921 for *E. packardi*, reported as *E. subopaca*; Collins 1980a for *E. gracilis*, reported as *E. cinerea*; and Herbst 1986 for *E. hians*). Distribution data were derived from Wirth (1971) and further supplemented by collection records and habitat chemistry data of the author.

RESULTS

Ecological and physiological limitations under changing salinity conditions in salt lakes appear to result in varied distribution and productivity of *Ephydra* spp. Distribution maps (Figs. 1, 2) and limited habitat data suggest high salinity conditions (usually $>25\ g \cdot L^{-1}$) favor *E. hians* in alkaline water and *E. gracilis* in chloride water. In low salinity ($<25\ g \cdot L^{-1}$) and ephemeral waters, *E. auripes* and *E. packardi* are often more common, again showing respective preferences for alkaline and chloride chemical conditions. The general prevalence of *E. gracilis* in the eastern, and *E. hians* in the western, Great Basin correspond to the trend in lake geochemistry being derived from eastern sedimentary vs. western igneous lithology in the generation of chemical profiles (Jones 1966, Fiero 1986). Habitats in which I have collected *E. auripes* and *E. packardi* are typically small, shallow seep and spring outflows onto saline playas, whereas *E. hians* and *E. gracilis* habitats are often large, deep perennial lakes or ponds. Within the Owens–Death Valley system of the southwest Great Basin, *E. auripes* is common in alkaline seeps around Owens Lake, while at the Death Valley terminus of these once-interconnected basins, *E. packardi* dominates the chloride waters of small seeps.

Comparisons of osmoregulation in *E. gracilis* and *hians* (Fig. 3) show that *E. gracilis* regulates hemolymph osmolality at an unusually high level for insects (700–1000 mOsm; Nemenz 1960), and about 3 times that found in *E. hians* (Herbst et al. 1988). The energetic cost of osmoregulation against this gradient may be calculated as shown by Potts and Parry (1964):

$$Calories = \sum_{\text{all solutes}} PA \cdot RT \cdot \ln \frac{C_h}{C_l} + nFE$$

where P and A refer to integumentary permeability and area, R is the gas constant, T is temperature, C_h and C_l are the high and low concentrations of the concentration gradient (external or internal), n is ion valence, F is Faraday constant, and E is the electrical potential difference. As a first approximation, the osmotic concentration gradient can be used to estimate energetic costs assuming cuticular permeability (P) and surface area (A) and electrical gradient (E) are similar for both species and chemical conditions, and all other units are constants; the relative cost becomes proportional to the natural log of the osmotic gradient C_h/C_l (Fig. 4). The cost functions shown indicate that *E. gracilis* may inhabit more saline waters because high hemolymph osmolality reduces the gradient, and relative cost is only about half that for *E. hians* at an equivalent external salinity. Chloride waters tend to be more hyperosmotic than carbonate because the osmotic concentration is higher for an equivalent TDS (g·L^{-1}) concentration.

While *E. gracilis* possesses physiological adaptation for life in high salinity chloride water, *E. hians* shows much greater tolerance for life in carbonate waters (alkaline soda lakes) than in chloride waters. LC-50 toxicity values occur at lower concentrations in chloride water than carbonate water (Figs. 5A, 5B). *E. hians* is adapted to alkaline carbonate lakes by virtue of the lime gland (Herbst and Bradley

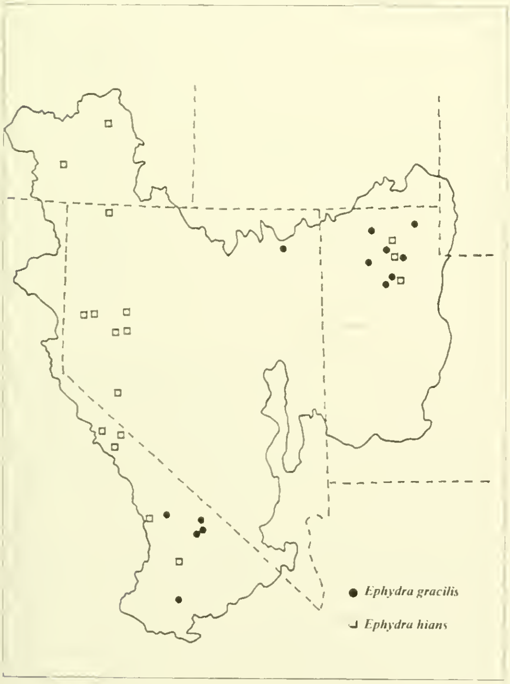

Fig. 1. Distribution of *Ephydra gracilis* and *Ephydra hians* within the hydrographic Great Basin. Based on Wirth (1971) and supplemental collections.

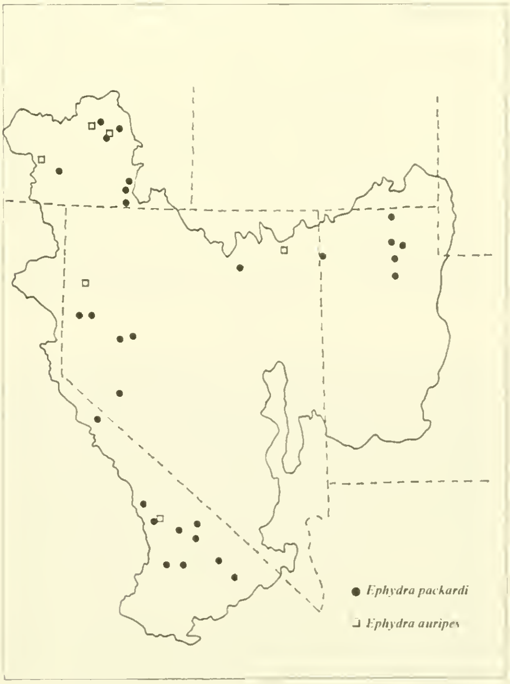

Fig. 2. Distribution of *Ephydra packardi* and *Ephydra auripes* within the hydrographic Great Basin. Based on Wirth (1971) and supplemental collections.

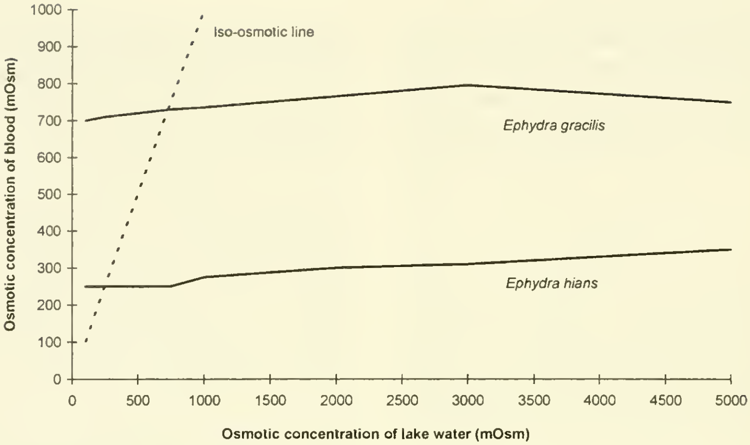

Fig. 3. Osmotic regulation in *Ephydra hians* (from Herbst et al. 1988) and *Ephydra gracilis* (from Nemenz 1960). Iso-osmotic line indicates where internal equals external concentrations.

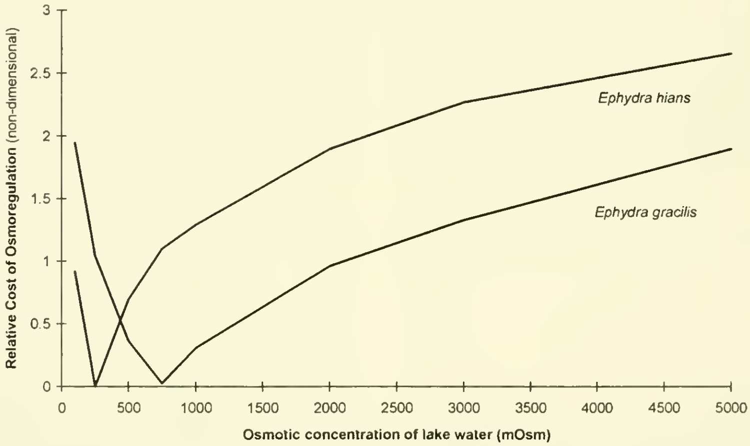

Fig. 4. Relative cost of osmoregulation in *Ephydra hians* and *Ephydra gracilis* based on osmotic gradient (cost is minimum where hemolymph and lake water are iso-osmotic).

1989). The lime gland is a modification of one pair of the Malpighian tubules in this species wherein calcium is concentrated and bicarbonate/carbonate are removed from the blood by forming a calcium carbonate precipitate within the tubules ("lime"). The intolerance shown by *E. hians* for chloride waters may indicate reduced capacity for regulating this anion though this species can survive in lower salinities of chloride water as suggested by the convergence of toxicity data for longer exposure times and lower salinities (Fig. 5).

Completion of a life cycle in ephemeral aquatic habitats involves such adaptations as resting stages or diapause, colonizing ability, and rapid development (Williams 1987). A comparative summary of ephydrid development rates in ephemeral vs. perennial habitats is given in Table 1. *E. packardi* has a short development time, comparable to *Scatella picea* from ephemeral ponds. This contrasts with the longer and more flexible development times seen in *E. gracilis* and *E. hians*, which may extend larval growth over long periods when exposed to the stress of reduced food availability or increased salinity. Species of temporary waters, without resting stages, do not have this option and must develop

TABLE 1. Duration of larval development in selected Ephydridae.

	Range of larval development time for instars 1–3 (days)	Habitat type	Reference
Ephydra packardi	11–13	ephemeral saline pools	Ping 1921
Ephydra gracilis	16–30 >100*	saline lakes	Collins 1980a
*Ephydra hians***	15–58 >120*	saline lakes	Herbst 1986
Scatella picea	4–11	ephemeral ponds	Connell and Scheiring 1982

*Under food limitation or salinity stress

**Range for populations from Mono and Abert lakes at 50 $g \cdot L^{-1}$ salinity and excess food

rapidly to reach maturity and disperse to new habitat. *E. packardi* exhibits this type of life history. In addition, *E. packardi* exhibits best growth at 40–50 $g \cdot L^{-1}$ and cannot survive above 90 $g \cdot L^{-1}$ (Ping 1921), well below the limits for *E. gracilis* or *E. hians*.

DISCUSSION

Based on the physiology and expense of salt tolerance, high salinity conditions favor *E. hians* in alkaline water and *E. gracilis* in chloride water. At lower salinities, based on limited habitat data, *E. auripes* and *E. packardi* are often more common, again showing respective preferences for alkaline and chloride chemical conditions. Specialized adaptations for alkaline carbonate waters are found in the larval Malpighian tubule lime gland of the alkali fly *E. hians*, while high salt tolerance in *E. gracilis* appears to be conferred by high hemolymph osmolality. Adaptation to ephemeral and low salinity conditions may be achieved by rapid larval growth rates as seen in *E. packardi*. Biogeographic patterns of association with chemical and regional differences in habitat types correspond with differing abilities of these *Ephydra* species.

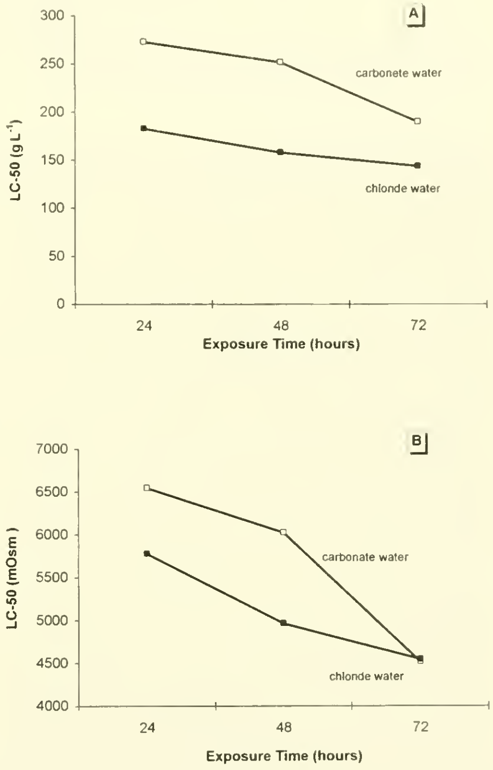

Fig. 5. Salt tolerance in third instar larvae of *Ephydra hians* exposed to saline waters where either carbonate or chloride are the dominant anions (from Herbst et al. 1988). LC-50 values are lethal concentrations at which half the exposed population dies as determined in mortality bioassays: A, expressed as total dissolved solids external salinity ($g \cdot L^{-1}$); B, expressed as external osmotic concentration (mOsm = milliosmolal).

While water chemistry may broadly define the distribution of *Ephydra* spp. among different habitat types, salinity changes within a habitat appear to control population production of species and the relative abundance of co-existing species. The intermediate salinity hypothesis (Herbst 1988) proposes that abundance of salt-tolerant organisms is limited by physiological stress at high salinities and by ecological factors, such as predation and competition, in more diverse communities at low salinities (Fig. 6). Field observations have provided evidence of changing population dynamics in fluctuating salt lakes. Increased abundance of *E. hians* at Mono Lake (California) and *E. gracilis* at Great Salt Lake (Utah) occurred during periods of salinity dilution (Winget et al. 1972, Herbst 1988). During a period of dilution of already low salinity at Abert Lake

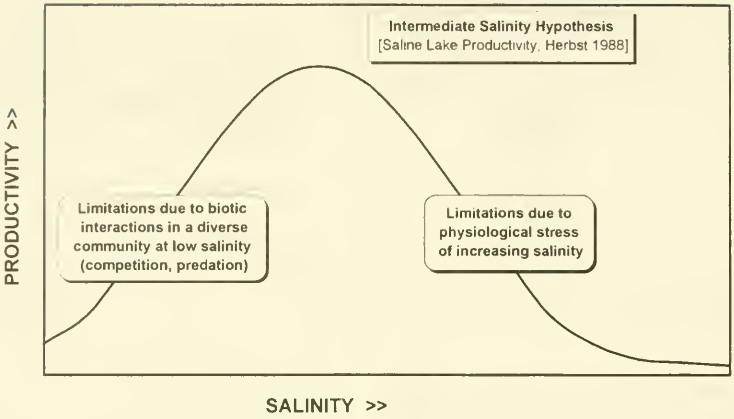
Intermediate Salinity Hypothesis
[Saline Lake Productivity, Herbst 1988]
PRODUCTIVITY >>
Limitations due to biotic interactions in a diverse community at low salinity (competition, predation)
Limitations due to physiological stress of increasing salinity
SALINITY >>

Fig. 6. Intermediate salinity hypothesis (Herbst 1988).

(Oregon), *E. hians* abundance was reduced in the presence of increasing numbers of other benthic invertebrates (Herbst 1988). Preliminary results of mesocosm salinity gradient experiments also support the intermediate salinity hypothesis (Herbst in preparation). Dilution of the chloride-rich waters of the Great Salt Lake has been followed by colonization and increased abundance of *E. hians*, where otherwise only *E. gracilis* was present (Welker and Havertz 1973, Collins 1980b). This last example suggests coexistence can occur within transitional regions of the physiological tolerance zones of *Ephydra* species.

Saline water habitats appear to be partitioned among the 4 species of Great Basin *Ephydra* along gradients of chemical composition, salinity, and stability (Fig. 7). This habitat template model (*sensu* Southwood 1977) predicts expected species distributions and potential changes in range and coexistence in space and time under varied environmental conditions. As a test of this conceptual model, further research on *Ephydra* spp. should include relating zoogeographic distributions to ionic tolerance and habitat chemistry using triangular anion diagrams, and comparisons of colonizing ability, life history traits, and population abundance along environmental gradients. For *E. auripes*, for which little data are available, the conceptual model predicts that this species has short development time, rapid colonization of new habitats, lower salt tolerance than *E. hians*, greater survival in carbonate than chloride chemistry, and poor competitive ability in coexistence with *E. hians*.

These data also might be applied to understanding other zoogeographic patterns in the Great Basin. Brine flies play a central trophic role in saline lakes as consumers of benthic algae, in turn providing one of the principal food sources used by migratory and breeding shorebirds and waterfowl (Jehl 1994, Rubega and Inouye 1994). The historical development of avian migratory routes and breeding colonies along the Pacific Flyway within the Great Basin during the Holocene may therefore be linked to salinity-related changes in the population production of *Ephydra* in different saline lake basins. Assuming that optimum production for *E. hians* is in the 25–100 $g \cdot L^{-1}$ range, and for *E. gracilis* in the 100–200 $g \cdot L^{-1}$ range, probable historical locations and changes of feeding grounds may be reconstructed from paleosalinity records alone.

Physiological and life history traits related to the selection regime of saline water habitats could provide distinctive characters for cladistics analysis and permit further investigation of the phylogenetic relationships in the genus *Ephydra* and other Ephydrinae (Mathis 1979a). Mathis separates *Haloscatella* from other subgenera of *Lamproscatella* partly on the basis of saline water habitat preferences, and it would be useful to examine further whether chemical tolerances among the species of the subgenus correspond to the cladogram presented (Mathis 1979b). The 5 Nearctic species of *Lamproscatella* (*Haloscatella*) spp. can be found within the Great Basin, and Mathis suggested that this is the zoogeographic origin of this group. Isolation through physiological adaptation to

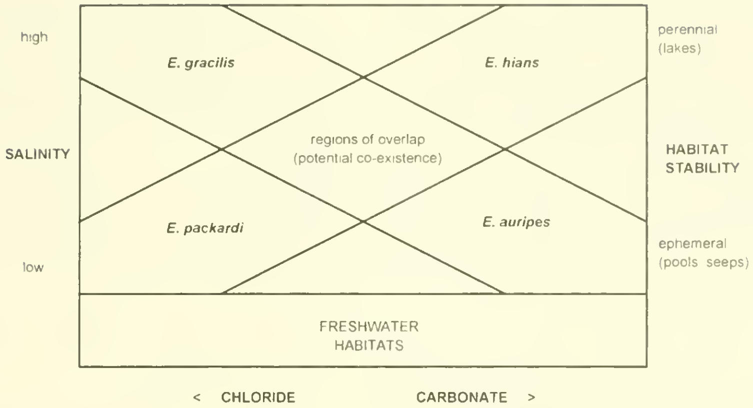

Fig. 7. Saline water habitat template for the distribution of Great Basin *Ephydra*. Each corner of environmental template inhabited primarily by a single species.

varied water chemistry may in fact be a more likely explanation for speciation and distribution in this group than through repeated vicariance through glaciation events as proposed by Mathis.

Other species in the genus *Ephydra* exhibit thermal adaptation. *E. geodeni* inhabits hot springs in freshwater to moderate salinities (Barnby 1987). *E. thermophila* and *E. bruesi* are endemics of acidic and alkaline thermal springs, respectively, in Yellowstone National Park (Collins 1977). Physiological adaptation and habitat partitioning along thermal, conductivity, and pH gradients may contribute to the origins and zoogeographic distribution of these species.

Other Ephydridae found in athalassic saline water habitats of the world may also exhibit biogeographic associations with geochemistry. Physiological adaptation to varied habitat geochemistry may exist in homologous ephydrid fauna in isolated desert regions such as the *Dimecoenia* spp. of the South American Altiplano, *Ephydrella* spp. of the Australian interior, and *Ephydra* spp. of the Old World (Wirth 1975).

Use of biological proxies as indicators of water chemistry of closed-basin lakes is well illustrated by the distribution of certain ostracode taxa in saline waters (Forester 1986). Species in the genus *Limnocythere* appear to have varied anionic preferences, with *L. staplini* found in chloride and sulfate waters, *L. sappaensis* in alkaline waters, and *L. ceriotuberosa* in waters of mixed chemistry. Another species, *Candona rawsoni*, is found only in low salinity alkaline water but can live in moderate salinities of sulfate water. These distributions suggest adaptations to different chemical conditions allow habitat partitioning. Fossil preservation of ostracodes permits their use as paleosalinity indicators. Other taxa with probable specific chemical-habitat affinities and potential for biogeographic interpretation through geochemistry include diatoms (Blinn 1994), corixids (Scudder 1976), and branchiopod crustacea (Bowen et al. 1985). Resh and Sorg (1983) have shown that lithium tolerance in the shore bug *Saldula usingerina* permits survival in certain thermal springs and can be used to predict local habitat distribution.

The remnants of pluvial Great Basin lakes are primarily saline bodies of water. Only a few perennial saline lakes remain (including Mono Lake, Abert Lake, Great Salt Lake, and Pyramid and Walker lakes), and many ephemeral ponds, wetlands, and spring seeps are also disappearing. Habitat loss has resulted primarily from stream diversion and spring development. Perennial lakes and ponds and other habitat refugia are threatened and must become part of a program of aquatic systems protection in the Great Basin to ensure the mosaic of habitats is available that has permitted the diversification of life such as is represented in the Ephydridae.

In conclusion, the following general syndromes of biogeographic patterns in the Great Basin are presented to reflect the importance of both vicariance and geochemical variation:

- obligate aquatic species (or those with poor dispersal ability) having restricted or endemic distributions (habitat isolation through vicariance);

- obligate aquatic species with widespread distributions (wide tolerance);
- vagile species with widespread distributions and wide habitat tolerance;
- vagile species with restricted distributions due to specialized adaptations for certain chemical or physical habitat conditions (e.g., *Ephydra*, others).

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STREAM TEMPERATURES AND THE ELEVATIONAL DISTRIBUTION OF REDBAND TROUT IN SOUTHWESTERN IDAHO

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ABSTRACT.—During July to September 1994–1996, I examined water temperatures at the lower end of the elevational distribution of redband trout (*Oncorhynchus mykiss gairdneri*) in 4 streams in the Owyhee Mountains in southwestern Idaho. Maximum water temperatures in Castle, Shoofly, Little Jacks, and Big Jacks creeks during low flows during a drought in 1994 ranged from 26.7°C to 29.0°C. Water temperatures fluctuated 9.5–11°C during the 24-h period maximum temperatures were observed. Stream flows at the lower end of Big Jacks and Little Jacks creeks in 1994 were <0.003 m^3 s^{-1} and subsided underground 50–130 m downstream of pools inhabited by trout. Trout were distributed to lower elevations where drainage basin area was larger in 2 of 3 yr ($P < 0.03$). Lower elevational limits of redband trout distribution in Big Jacks, Little Jacks, Castle, and Shoofly creeks were 920, 934, 972, and 1090 m above sea level, respectively, in 1994. With higher stream flows in 1995–96, trout were found 3–6 km farther downstream in Castle, Big Jacks, and Shoofly creeks at elevations of 860, 891, and 998 m, respectively, and tolerated maximum temperatures of 25.5–29.0°C. Trout were not distributed farther down Little Jacks Creek because of poor channel conditions. Maximum daily water temperatures of 29.0°C may have limited trout distribution in Big Jacks Creek, as flows and suitable channel conditions (but higher temperatures) continued >5 km downstream of the lowest pool inhabited by trout in 1995–96.

Key words: redband trout, Oncorhynchus mykiss gairdneri, *desert streams, water temperature, elevation, southwest Idaho, distribution.*

Redband trout (*Oncorhynchus mykiss gairdneri*) in desert basins of western North America are thought to have evolved adaptations to live in harsh environments characterized by extremes in water temperature and flow (Behnke 1992). However, little is known about the environmental extremes redband trout tolerate in desert streams. Redband trout were observed feeding at water temperatures of 28.3°C in Chino Creek, a tributary to the Owyhee River in northern Nevada (Behnke 1992). In contrast, rainbow trout (*Oncorhynchus mykiss irideus*) are typically stressed by water temperatures >22°C (Behnke 1992). Redband trout inhabit desert streams in the Snake River basin in southwestern Idaho. Many of these streams become intermittent at lower elevations, and flows fluctuate greatly year to year depending on winter snowpacks.

Knowledge of the maximum temperatures redband trout tolerate would assist fisheries managers in determining potential distribution of redband trout in streams in the Snake River basin in southwestern Idaho. With watershed restoration, redband trout may be able to inhabit more streams or extend their downstream distribution in occupied streams. Studies of the elevational distribution of redband trout in relation to water temperatures and stream flows are needed to determine if or how these parameters limit distribution. Stream flows and consequently trout distribution may also be influenced by watershed characteristics such as drainage basin area and elevation of source springs.

The objectives of this study were (1) to determine the lower elevational distribution of redband trout in 4 drainages typical of streams on the northeast slopes of the Owyhee Mountains that are tributaries to the Snake River, (2) to determine the maximum water temperatures trout were tolerating at the lower end of their distribution in these streams, and (3) to examine whether the size of the drainage basin affected the lower elevation to which trout were distributed in a stream. Additionally, I compared the distribution of redband trout and maximum water temperatures at the lower limit of their distribution between years of low stream flows in 1994 and average flow conditions in 1995 and 1996.

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STUDY AREA

I conducted the study on Big Jacks, Little Jacks, Shoofly, and Castle creeks, which flow northward from the Owyhee Mountains to the Snake River, near the town of Bruneau in southwestern Idaho (Fig. 1). Redband trout occupy the upper reaches of these streams, all 4 of which are usually intermittent at the lower end of the drainages and are moderately confined by side valley slopes with gradients of 1.5–4% (B channel types, Rosgen 1994; Table 1). Big Jacks and Little Jacks creeks and the upper portion of Shoofly Creek flow through 30- to 210-m-deep canyons with narrow floodplains and stream substrates dominated by cobble-sized rocks. Stream substrates in Castle Creek are primarily gravels and finer-sized particles as are the lower portions of Shoofly Creek. Streamside vegetation is dominated by willows (*Salix lasiolepsis*, *S. lasiandra*, *S. exigua*, and *S. lutea*). In areas of historical heavy livestock grazing and where flows become intermittent, streamside vegetation is composed of mesic forbs such as goldenrod (*Solidago* sp.) and grasses.

Little Jacks Creek is a tributary to Big Jacks Creek, but it rarely flows aboveground past a highly degraded, braided stream channel (D channel type; Rosgen 1994) starting 6.9 km upstream of its confluence with Big Jacks Creek. Big Jacks Creek flows to stream km 20.3 (site of a U.S. Geological Survey gaging station) 60% of the time (primarily during the

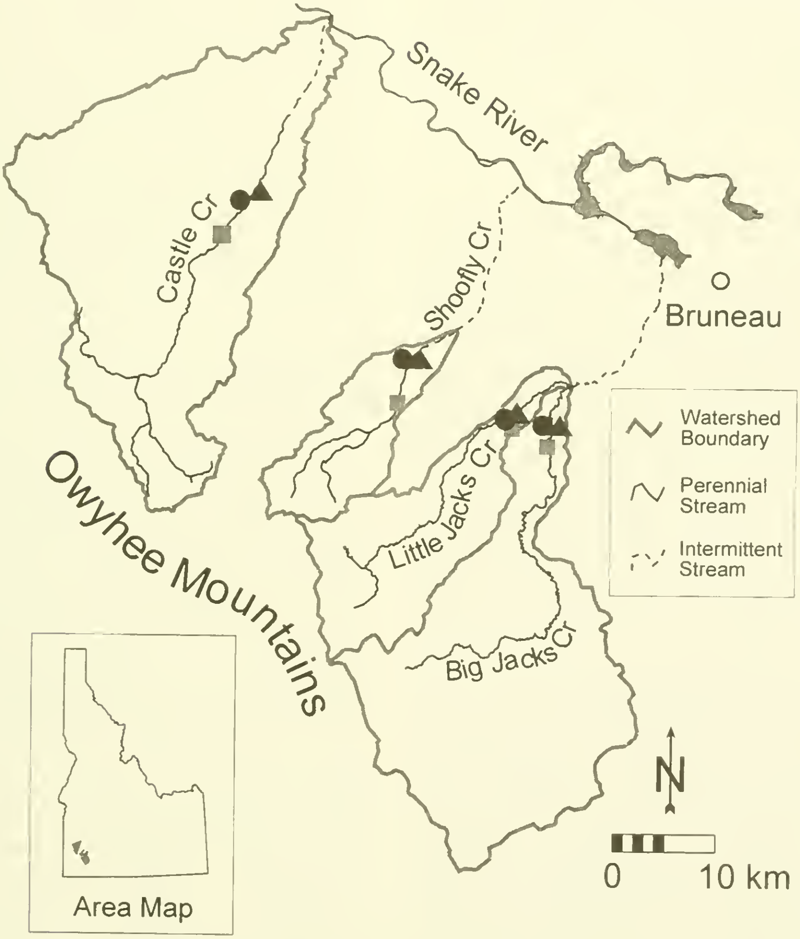

Fig. 1. Location of Castle, Shoofly, Little Jacks, and Big Jacks creeks in southwestern Idaho; their watershed boundaries; lower distributional limits of redband trout in the streams in 1994 (square symbols), 1995 (circles), and 1996 (triangles); and area map (inset).

TABLE 1. Characteristics of 4 drainages in which redband trout were studied in southwestern Idaho, 1994–1996.

Stream	Stream order	Drainage basin area (km²)	Geologic parent material	Elevation (m) Headwaters	Elevation (m) Confluence[a]
Big Jacks	3	633	rhyolite lava	1670	748
Little Jacks	2	260	rhyolite lava	1673	748
Shoofly	2	55	rhyolite lava	1639	724
Castle	3	790	granite/lava	1774	710

[a] Confluence of drainage with Snake River; Big Jacks and Little Jacks join to form Jacks Creek

months of January through June; Kjelstrom et al. 1995) and occasionally flows aboveground to the Snake River in early spring and during storm events. In 1992, Big Jacks Creek did not flow down to the gage site. Shoofly Creek also rarely flows to the Snake River. Flows in Castle, Big Jacks, and Shoofly creeks are diverted for irrigation at the lower end of the drainages where the streams enter broader valleys with associated low-gradient, unconfined channels (C channel type; Rosgen 1994).

METHODS

I visually observed redband trout at the lower end of each drainage in late June 1994–1996 to determine their approximate elevational distribution. I then used a Smith-Root Model 12-A backpack electrofisher to collect fish to determine the lower limit of distribution of redband trout in each stream. Pools that provided relatively high quality habitat (depths of 0.2–0.3 m with some cover) for redband trout were electrofished to determine if trout were present. I sampled downstream to where flows subsided underground or to 200 m downstream of the last pool where trout were encountered by electrofishing. Exceptions were Shoofly Creek, which was sampled only as far downstream as a private land boundary in 1994, and similarly Castle Creek in 1996. Trout may have been distributed farther down Castle Creek in 1996 and probably were distributed farther down Shoofly Creek in 1994.

I visually checked the presence of trout at the lower end of their distribution in Little Jacks Creek every 2 wk during the summer in 1994–95 and also on this schedule in Big Jacks Creek in 1994. Little Jacks Creek was observed monthly in 1996. All sites were rechecked for trout in September by electrofishing.

Trout density was estimated in July by electrofishing representative sites within 3 km of the lower limit of trout distribution. Two or 3 electrofishing passes were made and population sizes estimated for 60- to 80-km-long segments using the Zippin capture-removal model (Zippin 1958).

I placed a thermograph in or near the farthest downstream pool where redband trout were encountered. Pools were shallow enough that flows thoroughly mixed, resulting in no thermal stratification as determined from measurements with a hand-held thermometer. Thermographs were placed in the streams in late June 1994–1996 and monitored water temperatures through September. Water temperatures were recorded every 2 h, or the daily maximum, minimum, and average temperatures were recorded. Temperature readings of thermographs were checked against hand-held thermometers when they were set in the stream and again when they were retrieved.

In 1995 maximum-registering thermometers were placed at the lower end of the distribution of trout in Little and Big Jacks creeks. Thermographs were placed in these creeks in 1995 prior to electrofishing, and the thermographs were 50–2700 m upstream of the lower end of the trout distributions. Therefore, thermometers were used in addition to thermographs to measure maximum temperatures.

I measured stream flows with a pygmy flow meter using standard discharge measurement methods (U.S. Geological Survey 1977). Discharges were measured in late summer (August–September) to determine base flows. I also used U.S. Geological Survey (USGS) gage data from a station at stream km 20.3 of Big Jacks Creek to determine stream flows.

Elevations at the lower end of the trout distribution on each drainage were calculated from USGS 7.5-minute topographic maps.

Using least-squares linear regression, I examined the relationship between the lower elevation of trout distribution and drainage basin size. The relationship between lower elevation of occurrence and drainage basin area was examined for each year.

RESULTS

I electrofished 2.3, 2.9, and 1.4 km of stream near the lower limit of trout distribution in the 4 streams in 1994, 1995, and 1996, respectively. Trout were continuously distributed; pools providing some security or resting cover were almost always occupied by 1 or more trout. Densities were low, averaging 2.2 trout/100 m^2 of stream (range = 0.2 to 7 trout/100 m^2, $n = 4$) within 3 km of the lower limit of trout distribution in 3 streams in which I examined density (Big Jacks, Castle, and Shoofly creeks). Adult trout ranged from 146 mm to 231 mm in length; young-of-year trout were 50–75 mm long. All fish appeared healthy.

Trout were always present in September at the sites of their lower limit of distribution determined from electrofishing in late June and early July. Trout were also always observed at the lower limit of their distribution when monitored biweekly or monthly during July to September.

ELEVATIONAL DISTRIBUTION.—Elevations at the lower limit of redband trout distribution in 1994 were 920–1090 m (Table 2). Flows in Big Jacks Creek continued at <0.003 m^3 s^{-1} just 50 m farther downstream of the last pool inhabited by trout in 1994. Similarly, stream flows in Little Jacks Creek of <0.003 m^3 s^{-1} continued only 130 m into a highly degraded, braided stream channel (D channel type) below the last pool inhabited by trout. However, stream flows of about 0.01 m^3 s^{-1} continued another 4.3 km below the last pool inhabited by redband trout in Castle Creek. Trout were present in Shoofly Creek to at least an elevation of 1113 m, at the lower limit of public land on the stream. Flows in Shoofly Creek of 0.005 m^3 s^{-1} continued about 2 km downstream onto private land, and trout were likely present a portion of this distance to an elevation of about 1090 m.

Redband trout were distributed to lower elevations in 1995–96 when stream flows were about 5 times greater than in 1994 (Table 2, Fig. 1). Big Jacks Creek flowed 8.3 km farther downstream in 1995 than in 1994, with trout recolonizing about 1/3 (2.7 km) of this distance. Trout in Castle Creek were distributed 4.9 and 5.8 km farther downstream in 1995 and 1996, respectively, than in 1994. In 1996 trout in Castle Creek were distributed at least to a diversion at a private land boundary and may have occurred downstream of the diversion. Similarly, in 1995–96 trout in Shoofly Creek were distributed 2–3 km farther downstream than in 1994, to an elevation of 998 m where stream flows were diverted into an irrigation canal. Flows in Big Jacks Creek were greater in 1996, but the lower limit of trout distribution was unchanged from 1995 (Table 2).

Trout distribution in Little Jacks Creek in 1995–96 differed only slightly from 1994, with their distribution ending at the upper end of a highly degraded, braided stream channel. Even with greater stream flows in 1995 (Table 2), surface flows continued just 0.8 km into the degraded segment and did not provide pool habitat more than 200 m into the segment. Surface flows in 1996 continued about 2.5 km

TABLE 2. Stream flows (m^3 s^{-1}) and elevations (m) at lower distributional limits of redband trout in 4 southwestern Idaho streams, 1994–1996.

	Year					
	1994		1995		1996	
Stream	Elevation	Flow[a]	Elevation	Flow	Elevation	Flow
Castle Creek	972	0.01	871	0.08	859	—[c]
Little Jacks Creek	934	0.03	934	0.07	934	0.09
Big Jacks Creek	920	0.0[b]	891	0.03[b]	891	0.08[b]
Shoofly Creek	1090	0.005	998	0.03	998	0.03

[a] Streams gaged late summer (August–September) to estimate base flow

[b] Measured at U.S. Geological Survey gage station 8.3 km downstream of fish distribution limit in 1994

[c] No data

into the degraded channel and trout were distributed 150 m farther downstream.

The elevation to which trout were distributed was dependent on the area of the drainage basin of the stream in 1995 (R^2 = 0.95, df = 1,2; P = 0.03) and 1996 (R^2 = 0.96, df = 1,2; P = 0.02), but not in 1994 (R^2 = 0.41, df = 1,2; P = 0.36). Generally, the larger drainage basins provided flows that allowed occupancy of lower elevations. However, Castle Creek had the largest basin area (Table 1), but in 1994 trout extended their distribution to lower elevations in 2 of 3 other drainages.

STREAM TEMPERATURES.—Daily maximum temperatures ranged from 17.9°C to 29.0°C during 1994 (Fig. 2a). I may have missed sampling the maximum temperature in Castle Creek; due to equipment failure the thermograph did not operate until 5 August 1994. The median daily maximum temperature was 24.5°C, and the 95th percentile of daily maximum temperatures for 3 streams monitored from late June through August was 28.0°C. Maximum water temperatures for individual streams ranged from 26.7°C to 29.0°C (Table 3). Because trout in Shoofly Creek in 1994 were likely distributed downstream onto private land, they probably tolerated maximum temperatures >26.7°C, which were the maximum temperatures measured at the lower boundary of public land. Water temperatures fluctuated 9.5–11°C during the 24-h period maximum temperatures were observed in 1994. Average daily temperatures ranged from 21.0°C to 23.0°C (Table 3). Temperatures remained within 3°C of the maximum for 4–9 h (Fig. 3). For daily maximums ≥27°C, temperatures were above 26°C for 2.9–4.4 h.

In 1995 daily maximum temperatures ranged from 18.0°C to 28.0°C (Fig. 2b). I could not relocate the thermograph in Big Jacks Creek; the maximum temperature was measured with a maximum-registering thermometer. The median daily maximum temperature was

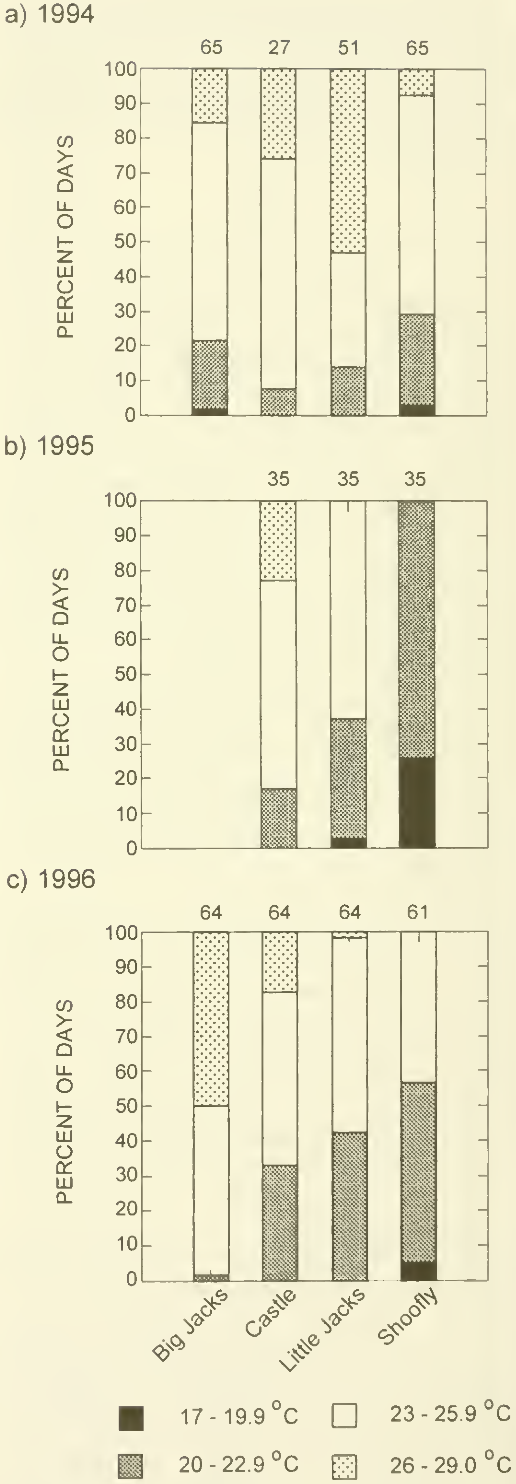

Fig. 2. Frequency distribution of daily maximum water temperatures at lower distributional limits of redband trout in 4 southwestern Idaho streams: (a) 29 June–31 August 1994, (b) 29 June–2 August 1995, (c) 29 June–31 August 1996. Number of days sampled is shown above the bar for each stream. Shoofly Creek was monitored at the same site in 1994–95 (5.7 km upstream of lower distributional limit in 1995). Big Jacks Creek was not monitored in 1995 due to equipment failure.

TABLE 3. Water temperatures during the 24-h period maximum temperatures were observed at the lower distributional limits of redband trout in 4 southwestern Idaho streams, 1994–1996.

	Temperature (°C)								
	1994			1995			1996		
Stream	Max.	Min.	Avg.	Max.	Min.	Avg.	Max.	Min.	Avg.
Castle Creek	27.0	17.0	22.5	26.5	18.5	21.0	27.0	19.0	22.5
Little Jacks Creek	29.0	17.9	23.0	25.0	18.5	21.0	26.0	19.2	22.1
Big Jacks Creek	27.9	18.5	21.3	28.0[a]	—	—	29.0	19.0	23.5
Shoofly Creek	26.7	15.5	21.0	22.5[b]	15.5	19.0	25.5	16.5	20.1

[a] Measured with a maximum-registering thermometer, mean and minimum temperatures not measured

[b] Monitored at same site as 1994 and 5.7 km upstream of lower distribution of trout in 1995

22.5°C, and the 95th percentile of daily maximum temperatures for the 3 streams monitored with thermographs was 26.0°C. Maximum water temperatures for individual streams ranged from 22.5°C to 28.0°C (Table 3). Water temperatures fluctuated 7–8°C during the 24-h period maximum temperatures were observed in 1995. Little Jacks and Shoofly creeks temperatures were monitored at the same sites in 1994–95. With greater stream flows in 1995 (Table 1), maximum water temperatures were about 4°C lower for the 2 streams (Fig. 2, Table 2). Because of poor stream channel conditions (wide and shallow with no pools), trout could not take advantage of the higher stream flows and move farther downstream in Little Jacks Creek in 1995–96.

Daily maximum temperatures in 1996 ranged from 18.5°C to 29.0°C between 29 June and 31 August (Fig. 2c). The median daily maximum temperature was 24.0°C, and the 95th percentile of daily maximum temperatures for all 4 streams was 28.0°C. Maximum water temperatures for individual streams ranged from 25.5°C to 29.0°C (Table 3). Water temperatures fluctuated 7–10°C during the 24-h period maximum temperatures were observed in 1996. The maximum temperature of 25.5°C observed in Shoofly Creek in 1996 was more representative of the maximum water temperatures experienced by trout at the lower end of their distribution. In 1995 temperatures were monitored in Shoofly Creek at the public land boundary 5.7 km upstream from the lower end of the distribution of trout. Maximum water temperatures observed at the lower distribution of trout in Big Jacks and Castle creeks were similar for all 3 yr (Table 3). Channel conditions were adequate in these 2 drainages to allow trout to move farther downstream during increased flows in 1995–96.

DISCUSSION

Pools at the lower ends of the 4 streams were shallow and did not thermally stratify. The continuous distribution of trout at the lower end of the drainages indicated thermal refugia from seeps were not present. Additionally, in 1994 I observed redband trout actively foraging at a temperature of 26.2°C in Big Jacks Creek 1 day before the stream reached its highest daily maximum temperature of 27.9°C. These observations indicate that trout were tolerating the temperatures measured at the lower limits of their distributions and not moving in and out of thermal refugia.

This is the first study to systematically document that redband trout in streams other than those in the Owyhee River basin tolerate extreme temperature fluctuations. Maximum temperatures tolerated by redband trout in this study (29°C) were slightly higher than Behnke (1992) observed for redband trout in Chino Creek in Nevada (28.3°C). Maximum water temperatures from this study were measured in streams with flowing water in contrast to Behnke's (1992) observation made at a pool remaining after stream flows stopped. Behnke (1992) states that tolerance of high temperatures shown by redband trout populations evolved through natural selection in streams of hot, arid regions over thousands of years. Redband trout inhabiting tributary streams to the Snake River in southwestern Idaho also demonstrated tolerance of low dissolved oxygen concentrations (1.6–4.0 mg L^{-1}) during periods of low stream flows (Vinson and Levesque 1994).

Rainbow and cutthroat trout (*Oncorhynchus clarki*) typically experience stress when water temperatures rise above 22°C. With gradual increases in temperature (1–2°C per day), loss

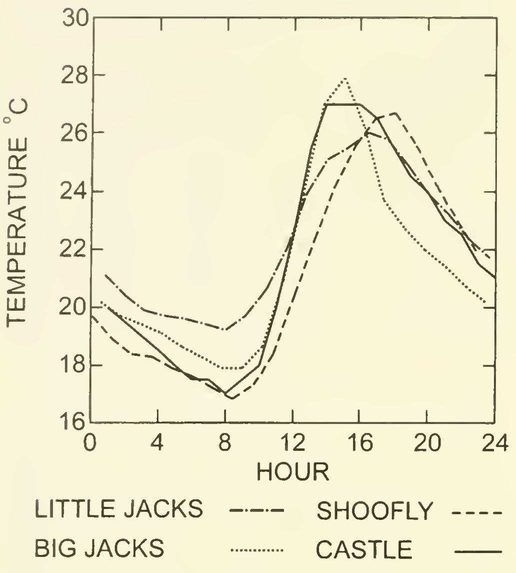

Fig. 3. Typical 24-h temperature cycle at the lower distributional limit of redband trout in Big Jacks (24 July 1994), Castle (5 August 1994), Shoofly (24 July 1994), and Little Jacks (13 August 1996) creeks in southwestern Idaho.

of equilibrium and death occur at about 28–29°C (Lee and Rinne 1980, Behnke 1992). Estimates of upper lethal temperatures for trout differ depending on the laboratory method used (Behnke 1992). Studies using long-duration exposures have estimated the upper lethal temperature for rainbow trout to be 26°C (Bidgood and Berst 1969, Charlon et al. 1970, Hokanson et al. 1977, Jobling 1981). Redband trout in the streams examined in this study tolerated greater daily fluctuations in temperature than used by Lee and Rinne (1980) to determine critical thermal maximum temperatures of 5 trout species. Rainbow, Apache (*Oncorhynchus gilae apache*), Gila (*Oncorhynchus gilae gilae*), and brown trout (*Salmo trutta*) tolerated fluctuations from only 21°C to 27°C when daily temperatures fluctuated 6°C over a 24-h period (Lee and Rinne 1980).

Redband trout in this study tolerated temperatures above 26°C for durations of up to 4.4 h. When the upper incipient lethal temperature of rainbow trout (25.6°C) was exceeded daily for 3 h under a fluctuating temperature regime (±4°C around a daily mean of 22°C), the daily mortality rate was 42.8% (Hokanson et al. 1977). Median resistance times from another laboratory study (Kaya 1978) indicated that 3 rainbow trout stocks acclimated to 17°C would tolerate a constant temperature of 26°C for 8.5–15.7 h with a 50% mortality rate and would tolerate 29°C for only 0.4 h.

The temperature range over which redband trout continue to feed and gain weight (functional feeding temperatures) may be a more important adaptation than an increase in the upper lethal temperature that is tolerated (Behnke 1992). Redband trout from a desert basin (Catlow Valley) in eastern Oregon had optimum growth efficiencies at temperatures >19°C, while growth rates of other *Oncorhynchus mykiss* stocks decrease with increasing temperatures above 16°C (Behnke 1992). Higher functional feeding temperatures would allow redband trout to maintain a competitive advantage over other fish species such as redside shiners (*Richardsonius balteatus*), which are common in warmer, low-elevation segments of streams in the Snake River basin.

During years of greater stream flows, redband trout were distributed farther downstream than during drought years, reoccupying 3- to 6-km sections of Castle, Shoofly, and Big Jacks creeks that had been totally dewatered 1 or 2 yr previously. However, the reoccupation of newly available sections of stream complicates determinations of whether or not maximum water temperatures limit distribution of redband trout. During years of greater snowpacks when surface flows continue farther down a drainage, trout may not be present because they have not yet recolonized the newly watered segment. In general, trout were distributed downstream to reaches with maximum temperatures of 27.0–29.0°C, provided channel conditions allowed trout to move downstream.

Poor channel conditions and subsiding of surface flows into streambed gravel limited trout distribution in Big Jacks Creek in 1994 and Little Jacks Creek during 1994–1996. Stream flows at the lower end of Big Jacks and Little Jacks creeks were <0.003 m^3 s^{-1}; redband trout were essentially distributed the length of surface flows in these 2 streams in 1994. Similarly, trout in Shoofly Creek in 1995–96 were distributed down to a stream diversion, which was the lower limit of available habitat. However, redband trout were not distributed the length of surface flows in Castle Creek in 1994–1996. In 1994, Castle Creek flowed at about 0.016 $m^3 s^{-1}$ for another 4.3 km below the last pool inhabited by trout. Water temperatures may have been a factor influencing the lower limit of the distribution of redband trout in Castle Creek. Maximum water temperatures of 29°C may have also limited redband trout distribution in Big Jacks Creek in 1996, as surface flows continued >5.6 km downstream of the lower distribution of trout.

During years of greater flows and consequently lower stream temperatures, trout in Little Jacks Creek were not able to move farther downstream because of poor watershed conditions. A highly braided D stream channel stopped trout recolonization of the lower drainage, probably because the shallow riffle habitat did not provide resting or hiding cover and also was quickly heated by solar radiation. This indicates that stream restoration on the lower ends of drainages in southwestern Idaho has the potential to increase the range and numbers of redband trout populations.

Trout populations may also be reconnected by improving habitat conditions at the lower end of drainages so that fish can move between some drainages, such as Big and Little Jacks creeks. Given current land uses and irrigation diversions, trout populations probably cannot be interconnected via the Snake River. In 1995–96, during typical stream flows for Big and Little Jacks and Castle creeks, redband trout were distributed only down to 860–900 m elevation. The confluence of these streams with the Snake River was at about 750 m elevation. The lower elevation of trout distribution was not significantly related to drainage basin area during low flows in 1994. However, during normal flows in 1995–96, trout were distributed to lower elevations as drainage basin area increased, probably because larger basins provided greater stream flows and lower stream temperatures to lower elevations.

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EFFECT OF SALINITY ON SEED GERMINATION OF *TRIGLOCHIN MARITIMA* UNDER VARIOUS TEMPERATURE REGIMES

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ABSTRACT.—*Triglochin maritima* L. (arrow grass), an herbaceous perennial in the family Juncaginaceae, is widely distributed in inland and coastal salt marshes of North America. *Triglochin maritima* seeds from a population growing in a salt marsh at Faust, Utah, were germinated at 4 temperature regimes (12-h night/12-h day, 5–15°C, 5–25°C, 10–20°C, and 15–25°C) and 5 salinities (0, 100, 200, 300, 400, and 500 mol m^{-3} NaCl) to determine optimal conditions for germination and level of salt tolerance. Ungerminated seeds were returned to distilled water after 20 d to determine whether seeds could recover from salinity treatments. Maximum germination occurred in distilled water, and increases in NaCl concentration progressively inhibited seed germination. No seeds germinated at concentrations higher than 400 mol m^{-3} NaCl. A temperature regime of low night (5°C) and high day (25°C) temperature yielded maximum germination; all other temperature regimes significantly inhibited seed germination relative to this optimum. Recovery of germination was highest at 5–25°C and lowest at 5–15°C. Recovery of seed germination when seeds were transferred to distilled water from salt solutions was highest at 5–25°C (72%) for seeds exposed to the 500 mol m^{-3} NaCl pretreatment and significantly reduced at other temperature regimes. The recovery germination response indicates a synergistic inhibitory interaction effect on germination when seeds were exposed to high salinities at suboptimal thermoperiods.

Key words: Triglochin maritima, *halophyte, recovery, seed germination, thermoperiod, Utah.*

Triglochin maritima L. (Juncaginaceae), commonly known as arrow grass, is a clonal perennial that can form regular clumps up to 2 m across and 60 cm high (Davy and Bishop 1991). Common in saline habitats, particularly coastal marshes on rocky shores in temperate, subarctic, and arctic regions, it also extends southward to the subtropics (Davy and Bishop 1991). *Triglochin maritima* is distributed in inland and coastal brackish and freshwater marshes and bogs of North America (Sheltler and Skog 1978). Ungar (1974) surveyed a *Triglochin maritima* community located at Park County, Colorado, and reported that *T. maritima* grew in almost pure stands in a wetter area with soil salinity ranging from 0.5% to 1% (85–170 mol m^{-3}). *Triglochin maritima* was also found growing in salt marshes at the Fish Springs research site, Juab County, Utah, in an *Eleocharis* meadow community where salinity averaged 0.5% total salts (Bolen 1964).

Germination of halophytes is affected by temperature and soil salinity content, and seeds are characterized by varying types and degrees of dormancy (Binet 1965, 1968, Ungar 1991). Binet (1959) reported that seeds from a French population of *T. maritima* had a primary morpho-physiological dormancy and that seeds of *T. maritima* were more dormant than *T. palustris*, probably because of the more resistant sclerenchyma tissue in the pericarp of the former. The 2 basic types of dormancy that seeds develop are due either to some morphological or biochemical characteristics of the diaspore that produce a primary dormancy (fruit or seed) or to an environmental factor that induces seeds into a secondary dormancy (Bewley and Black 1982). Binet (1961a, 1961b) reported that *T. maritima* had a secondary dormancy induced by darkness, which in nature is probably triggered by the burial of seeds in the soil.

Germination responses of seeds of *T. maritima* populations from North America have not been previously investigated, and one of the goals of this investigation was to determine if responses to environmental variables differ from populations studied from Europe and related species from Africa. Naidoo and Naicker (1992) studied the effect of light, temperature, and salinity on the germination of *T. bulbosa* and *T. striata* populations from South

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Africa and determined that both species have a light requirement for germination and achieve higher germination at a warmer temperature regime (20–30°C). Germination was highest in distilled water and decreased significantly with an increase in salinity up to 500 mol m^{-3}. Transfer of ungerminated, salt-treated seeds to distilled water stimulated germination more in *T. striata* than in *T. bulbosa*. The interaction between salinity and temperature on germination has been the subject of investigation (Khan and Ungar 1984, Gutterman 1986, Khan and Weber 1986, Khan et al. 1987, Badger and Ungar 1989, Khan 1991, Khan and Rizvi 1994) because it plays a significant role in determining the timing of germination. However, no data are available concerning the effect of the interaction between different temperature regimes and salinity on seed germination of North American populations of *T. maritima*. These 2 environmental factors play a significant role in determining whether plants can successfully establish in saline habitats because they interact in determining if seeds germinate or remain dormant in the seed bank (Ungar 1995). One of the purposes of this investigation was to determine how the germination response of *T. maritima* to temperature and salinity may affect its establishment in salt marsh habitats.

Recovery germination of seeds in freshwater after they were exposed to saline conditions has been investigated (Ungar 1962, 1978, Barbour 1970, Parham 1970, Macke and Ungar 1971, Seneca and Cooper 1971, Woodell 1985, Keiffer and Ungar 1995) to determine if seeds can remain viable after being exposed to hypersaline conditions, but no similar data are available for *T. maritima* seeds. The ability of seeds to germinate after exposure to hypersaline conditions plays a significant role in the establishment of halophyte populations. Seeds of glycophytes cannot germinate after exposure to salt stress, while halophytes show a range of responses from partial to complete germination recovery when salinity stress is alleviated (Woodell 1985, Ungar 1991).

This study was initiated to obtain a better understanding of germination requirements of seeds of a population of *T. maritima* from the Great Salt Lake region of Utah. Initial establishment of species in salt marsh habitats is related to germination response of seeds to salinity and temperature regime and usually determines if a population will survive to reproductive maturity. Each species has very specific germination requirements, and its response to stress varies from that of other species. For this reason it is important to determine the range of tolerance to salinity and temperature regime effects on germination. The effects of salinity and temperature regime on germination and recovery responses of *T. maritima* were studied to determine their individual effects and any interaction between these factors on seed germination. We also determined if salinity and temperature regime interact in their effects on recovery germination of seeds initially exposed to saline conditions.

MATERIALS AND METHODS

We collected *Triglochin maritima* L. seeds during August 1995 from a salt marsh situated 30 mi south of the Great Salt Lake, at Faust, Utah. Seeds were separated from the inflorescence and brought to Ohio University where they were stored at 4°C. Preliminary tests indicated the seeds were viable and germination experiments were initiated in September 1995 in 50 × 9-mm (Gelman No. 7232) tight-fitting plastic petri dishes with 5 ml of test solution. Each dish, containing 25 seeds that were surface sterilized with the fungicide Phygon, was placed in a 10-cm-diameter plastic petri dish as an added precaution against water loss by evaporation. Four petri dishes containing 25 seeds each were used as replicates for each salinity and temperature treatment; seeds were considered to be germinated with the emergence of the radicle.

To determine the effect of temperature on germination, we used regimes of 5–15°C, 5–25°C, 10–20°C, and 15–25°C. We used a 24-h cycle, where the higher temperature (15, 20, or 25°C) coincided with the 12-h light period (Sylvania cool white fluorescent lamps, 25 μmol m^{-2} s^{-1}, 400–750 nm) and the lower temperature (5, 10, or 15°C) coincided with the 12-h dark period. Seeds were germinated in distilled water, 100, 200, 300, 400, and 500 mol m^{-3} NaCl solutions in each of the temperature regimes, and germination was recorded every other day for 20 d. After 20 d we transferred ungerminated seeds from the NaCl treatments to distilled water and a temperature regime of 5–25°C to determine the recovery germination, which was also recorded at

TABLE 1. Results of a 2-way ANOVA of final percent germination of *Triglochin maritima* in different salinity and temperature treatments.

Source of variation	Sum of squares	df	Mean square	*F*	Significance of *F*
Temperature	10327.3	3	3442.4	72.4	0.0001
Salinity	17729.3	5	3545.9	74.6	0.0001
Temperature × salinity	7702.7	15	513.5	10.8	0.0001

2-d intervals for 20 d. Rate of germination was estimated by using a modified Timson index of germination velocity (TI = $\sum G/t$), where G is the number of seeds germinating at 2-d intervals and t is the total germination period (Khan and Ungar 1984). The maximum value possible using this index with our data was 50 (i.e., 1000/20), and the higher the value, the more rapid the rate of germination.

Germination data were transformed (arcsine) before statistical analysis and data were analyzed with a 2-way ANOVA using SPSS for Windows, release 6.1 (SPSS Inc. 1994).

RESULTS

Different temperature regimes, salinity, and their interaction significantly ($P < 0.0001$) affected the final percent germination of *T. maritima* seeds (Table 1). Germination of *T. maritima* was highest in distilled water and at a regime with low night (5°C) and high day (25°C) temperatures (Fig. 1). Maximum germination percentages were achieved in 12 d in all treatments. Germination of seeds decreased with increases in salinity; few seeds germinated at salt concentrations higher than 300 mol m^{-3} NaCl (Fig. 1). Variation in temperature regime significantly affected seed germination under both saline and non-saline conditions. In fact, there was less than 10% germination at the 5–15°C temperature regime in the control and all salinity treatments (Fig. 1). At other temperature regimes there was a significant inhibitory interaction between temperature and salinity on final germination percentages (Table 1, Fig. 1).

Different temperature regimes, salinity, and their interaction significantly ($P < 0.0001$) affected the rate of germination of *T. maritima* seeds as determined from the Timson index of germination velocity (Tables 2, 3). The rate of germination, calculated using a modified Timson index of germination velocity, was lowest in 5–15°C and highest in 5–25°C (Table 2). At temperature regimes of 10–20°C and 15–25°C, the rate of germination was similar in the controls, but the interaction caused by the addition of NaCl to the medium adversely affected the germination rate at 10–20°C (Tables 2, 3).

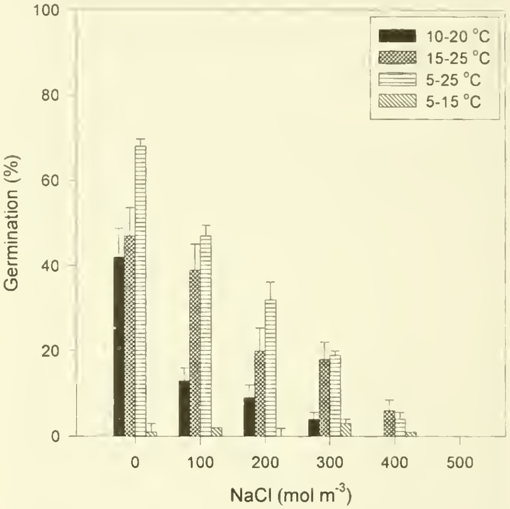

Fig. 1 Percent germination of *Triglochin maritima* seeds in 0, 100, 200, 300, 400, and 500 mol m^{-3} NaCl at temperature regimes of 5–15°C, 5–25°C, 10–20°C, and 15–25°C.

After 20 d of NaCl treatment, seeds were transferred to distilled water, where there was less than 25% recovery germination in the 10–20°C temperature regime at all NaCl concentrations (Fig. 2). At 15–25°C and 5–25°C the final germination percentages increased to more than 50% at 500 mol m^{-3} NaCl. Recovery at the highest salinity concentration (500 mol m^{-3}) was lower than that in the 400 mol m^{-3} NaCl treatment, which did not differ significantly from the control at 5–25°C (Fig. 2). Ungerminated seeds from the 5–15°C temperature regime were transferred to 5–25°C after 20 d and germination increased, but germination was significantly lower than for those seeds that initially germinated at 5–25°C (Fig. 2).

TABLE 2. Index of germination velocity, using a modified Timson index (Khan and Ungar 1984) to estimate rate of germination of *Triglochin maritima*.

NaCl (mol m^{-3})	Temperature regime (°C)			
	10–20	15–25	5–25	5–15
0	15.7 ± 2.3	17.8 ± 3.4	24.1 ± 3.3	0.7 ± 0.7
100	4.2 ± 2.3	12.4 ± 2.4	16.4 ± 0.8	0
200	2.7 ± 0.8	6.6 ± 1.7	9.6 ± 1.2	0.4 ± 0.3
300	1.2 ± 0.5	5.0 ± 1.2	4.5 ± 0.4	0.1 ± 0.1
400	0	1.7 ± 0.7	0.5 ± 0.2	0
500	0	0	0	0

TABLE 3. Results of a 2-way ANOVA, using data from the Timson index of germination velocity to estimate rate of germination of *Triglochin maritima* at different salinities and temperatures.

Source of variation	Sum of squares	df	Mean square	*F*	Significance of *F*
Temperature	1118.4	3	372.8	51.2	0.0001
Salinity	2434.5	5	486.9	66.9	0.0001
Temperature × salinity	1016.9	15	67.8	9.3	0.0001

Recovery germination percentages increased with an increase in salinity concentration (Fig. 3). At a temperature regime of 10–20°C, a maximum of 20% recovery germination was obtained in 500 mol m^{-3} NaCl, but seeds treated with 400 mol m^{-3} NaCl at 5–25°C had 72% recovery (Fig. 3).

DISCUSSION

Triglochin maritima germination is most probably regulated through variation in soil salinity and temperature regime under natural conditions. When soil salinity is beyond the levels at which seeds can germinate, seeds may die or remain dormant in the soil seed bank. Seed germination can then take place at a later time in the growing season or in another year after salt stress has been alleviated (Ungar 1995). Bolen (1964) and Ungar (1974) reported that *T. maritima* was found growing in communities with moderate salinity, 0.5–1.0% total salts (85–170 mol m^{-3}). We determined that seeds from the Utah population required low soil salinity and a temperature regime with low night (5°C) and high day temperatures (25°C) to promote maximum germination. Binet (1959) reported that freshly collected *T. maritima* seeds enclosed by the pericarp had an innate dormancy and poor germination in the dark (Parham 1970). Our results indicate that seeds of this Utah population were not dormant and that germination was inhibited by high salinities and low day temperatures. We determined that *Triglochin maritima* seeds had their highest germination percentages in distilled water and a progressive decline in germination with increases in salinity. Similar results were found in populations from Europe (Binet 1960, 1965, Pigott 1969, Lotschert 1970). Our results agree with those of Binet (1965), who determined that germination in saline media of seeds from a French population of *T. maritima* was greatly facilitated by alternating temperature regimes of 5–25°C, which can substitute substantially for the light requirement. Likewise, germination of the related species *Triglochin bulbosa* and *T. striata* was also highest in non-saline controls and decreased significantly with an increase in salinity up to 500 mol m^{-3} (Naidoo and Naicker 1992). Higher day temperatures were more stimulating for germination compared to lower thermoperiods in all of these species of *Triglochin*. Similar promotive effects of high daytime temperatures on germination also were found in other perennial halophytes such as *Cressa cretica* (Khan 1991), *Atriplex griffithii* (Khan and Rizvi 1994), *Salicornia pacifica* var. *utahensis* (Khan and Weber 1986), *Halopyrum mucronatum*

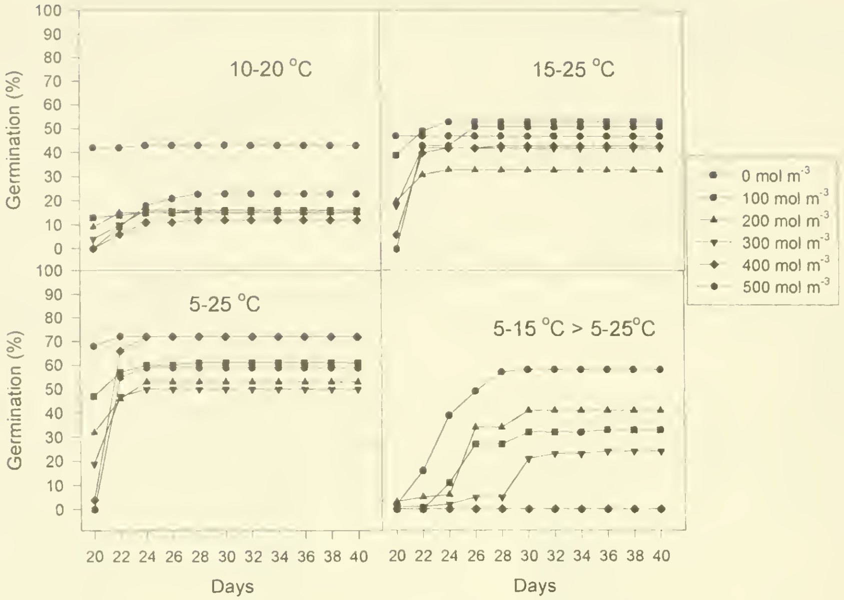

Fig. 2. Percent germination of *Triglochin maritima* seeds after being transferred from 0, 100, 200, 300, 400, and 500 mol m^{-3} NaCl at temperature regimes of 5–15°C, 5–25°C, 10–20°C, and 15–25°C.

(Noor and Khan 1995), and *Chrysothamnus nauseosus* (Khan et al. 1987).

Seeds of *Triglochin maritima* from the Utah population, when transferred to distilled water after a 20-d treatment at various salinity concentrations, responded differentially under different temperature regimes. There was little recovery (20%) with the 10–20°C temperature regime in non-saline controls, but at 5–25°C seeds incubated previously at 400 mol m^{-3} NaCl had about 72% recovery. It seems that recovery germination of *T. maritima* is temperature dependent. Binet (1961b) determined that seeds of *T. maritima* from a French coastal population had a stratification and light requirement, and when immersed in seawater at 3°C for 60–80 d, they were capable of germinating subsequently in freshwater upon transfer to 25°C in the light or dark. Seeds from the Utah population did not require stratification and were not dormant. Woodell (1985) included *T. maritima* in the group of coastal species whose subsequent germination is stimulated by exposure to high salinity, although the germination percentages he recorded were low. Our results indicate the recovery germination response of *T. maritima* seeds in distilled water after 20 d exposure to 500 mol m^{-3} NaCl was temperature dependent. Keiffer and Ungar (1995) exposed seeds of 5 halophytes (*Atriplex prostrata*, *Hordeum jubatum*, *Salicornia europaea*, *Spergularia marina*, and *Suaeda calceoliformis*) to salinity treatments for 2 yr and determined their recovery responses when transferred to distilled water. They used the Woodell (1985) classification system and placed *Atriplex prostrata* seeds in Type 1 (recovery inhibited by high salinity), *Hordeum jubatum* and *Spergularia marina* in Type 2 (recovery equal to original controls), and *Salicornia europaea* and *Suaeda calceoliformis* in Type 3 (salt stimulated, recovery greater than controls). Our data from the 500 mol m^{-3} NaCl treatment indicate that *T. maritima* recovery germination could be classified in Type 1 (10–20°C) or Type 2 (15–25°C), depending on the temperature regime used in the recovery germination experiment. Seeds exposed to 5–15°C in all salinity treatments had low recovery germination percentages.

Triglochin maritima seeds had maximum germination at a 5–25°C temperature regime at all NaCl concentrations tested. Few seeds germinated at the 5–15°C in non-saline controls. Inability to germinate at low day temperature in the laboratory indicates that a

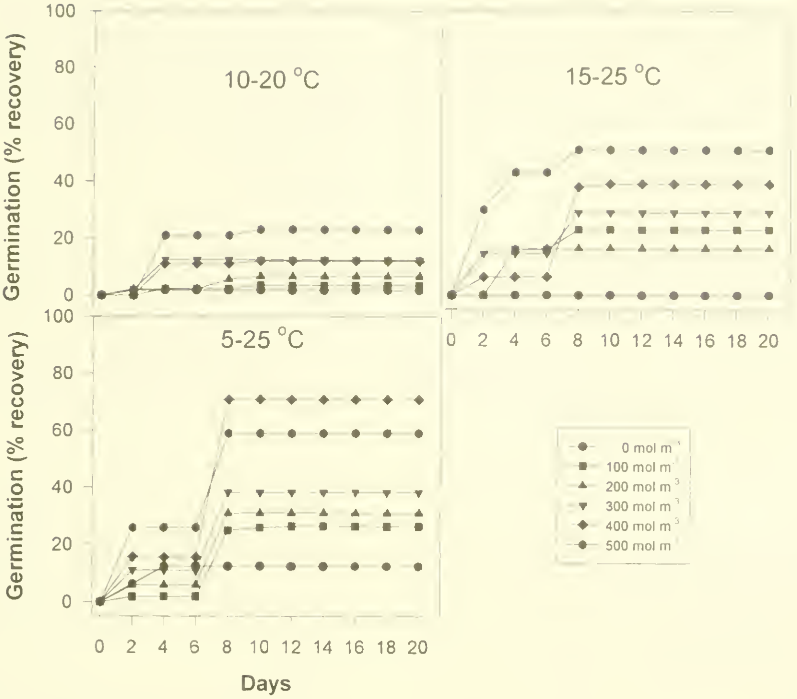

Fig. 3. Percent recovery germination in freshwater of ungerminated *Triglochin maritima* seeds initially exposed to 0, 100, 200, 300, 400, and 500 mol m^{-3} NaCl at temperature regimes of 5–25°C, 10–20°C, and 15–25°C.

threshold of higher day temperatures is necessary to stimulate germination under field conditions. A combination of reduced salinity and high daytime temperatures stimulates germination and determines the sites along salinity gradients where germination and establishment of *T. maritima* can occur. Because soil salinity stress usually increases during the summer months, salinity conditions early in the growing season at the germination stage determine whether halophytes will be able to successfully establish at a site (Ungar 1995). Recovery germination responses were also dependent on temperature, ranging from 0% recovery at 5–15°C to 72% at 5–25°C. Seeds of *Triglochin maritima* will germinate when soil salinity is low and the temperature regime is appropriate under natural conditions, or they will remain dormant in the seed bank until soil salinity is reduced and an appropriate temperature regime occurs. Our laboratory investigations with seeds from this Utah population more precisely define the temperature and salinity conditions necessary for maximum germination and recovery of seeds of *T. maritima* from hypersaline conditions. Seeds were not dormant but did have specific temperature requirements for maximum germination.

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AN IRVINGTONIAN SPECIES OF *BRACHYLAGUS* (MAMMALIA: LAGOMORPHA) FROM PORCUPINE CAVE, PARK COUNTY, COLORADO

Colleen N. Ramos[1]

ABSTRACT.—*Brachylagus* is currently a monotypic genus of uncertain origins and known only from Holocene and late Rancholabrean. A new species of leporid is described from the early and middle Pleistocene (Irvingtonian) deposits of Porcupine Cave, Park County, Colorado. Stratified deposits of the Pit and the Velvet Room, 2 localities within Porcupine Cave, have been dated biochronologically and paleomagnetically from the middle Irvingtonian and early to middle Irvingtonian, respectively. *Brachylagus coloradoensis*, sp. nov., is characterized by its conserved p3 enamel patterns which are intermediate between *B. idahoensis* and *Hypolagus*, and its size which is slightly larger than that of *B. idahoensis*. This suggests a possible ancestral relationship between *Hypolagus* and *Brachylagus*.

Key words: Brachylagus, *Irvingtonian*, Brachylagus idahoensis, *pygmy rabbit*, *Leporidae*, *Lagomorpha*, *Pleistocene*.

Brachylagus idahoensis (pygmy rabbit), the sole living species of *Brachylagus*, is a small rabbit that is restricted to dense stands of sagebrush (*Artemisia* spp.) in the Great Basin. An isolated population also survives in eastern Washington and is currently the subject of attention by conservationists. Because of its highly specific habitat needs (as reviewed by Dobler and Dixon 1990), the species is vulnerable to local extirpation as its natural habitat is modified and/or destroyed by agriculture and cattle grazing. The species has apparently existed in the Great Basin area for much of its evolutionary history as only a single paleontological site is known from outside its current range (Walker 1987).

The genus has a long history of taxonomic uncertainty but is now generally considered to be valid. The species now known as *B. idahoensis* was first described by Merriam (1891) but ascribed to the genus *Lepus*. Miller (1900) formally proposed the subgenus *Brachylagus*, which Lyon (1904) elevated to full generic status, a usage maintained by Nelson (1909). Later authors placed the species in the genus of *Sylvilagus* (Grinnell et al. 1930, Orr 1940, Durrant 1952). More recent morphological work has supported the generic status of *Brachylagus* (Kenner 1965), with recent genetic work (reviewed by Chapman and Ceballos 1990) further substantiating this.

Brachylagus idahoensis, being the smallest leporid in North America, is easily identified by its unique p3 enamel patterns and its small size. Even so, few paleontological sites include this species in their faunal lists; thus, it has a limited fossil record that extends only to the late Rancholabrean (Kurtén and Anderson 1980). However, material from Cathedral Cave, an Irvingtonian site in eastern Nevada, has yielded isolated teeth easily referable to *B. idahoensis* (C.J. Bell personal communication). Despite its limited geologic presence, this genus has been hypothesized to have originated either in the Miocene and descended from the genus *Alilepus* (Hibbard 1963), or later in the Pliocene and again derived from *Alilepus* (White 1991b). These hypothetical ancestries are based upon formation of the p3 enamel pattern found in *Brachylagus*, which is completely distinct from other North American leporids. Given the limited fossil record of *Brachylagus* and extensive radiation of the genus *Hypolagus* during the Pliocene, a reasonable, alternative hypothesis is that *Brachylagus* arose directly from *Hypolagus* in the late Blancan or early Irvingtonian. These hypotheses are summarized in Figure 1 and evaluated below.

The species described here occurs in the Irvingtonian deposits of Porcupine Cave, Park County, Colorado. The cave contains several

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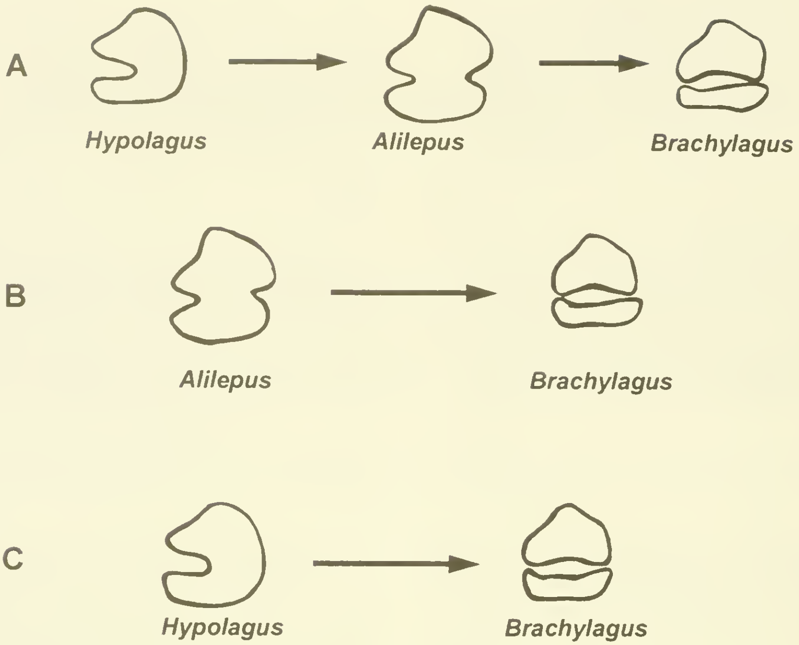

Fig. 1. Summary of hypotheses concerning evolution of p3 form seen in *Brachylagus*: A, *Brachylagus* descending from *Alilepus*, posterior-external reentrant (PER) fuses with posterior internal reentrant to form separate lobes as seen in *Brachylagus* (summarized from Hibbard 1963); B, *Brachylagus* descending from *Alilepus* (which arose from *Hypolagus*) during late Pliocene or early Pleistocene (after White 1991b); and C, *Brachylagus* descending directly from *Hypolagus*, PER eventually extends completely across width of the tooth to separate the trigonid from the talonid.

rooms from which fossils have been collected (Barnosky and Rasmussen 1988, Wood and Barnosky 1994, Anderson 1995). These rooms and areas represent localities within Porcupine Cave and include the Pit, Velvet Room, and Mark's Sink. Fossil deposits range in age from early to late Irvingtonian. The Pit, a small room in the cave, was excavated by the Carnegie Museum (CM) in the 1980s and was originally thought to date between approximately 0.38 my to roughly 0.8 my (Barnosky and Rasmussen 1988, Wood and Barnosky 1994). More recent analyses date the majority of the Pit around 850,000 y.b.p. (Barnosky personal communication). Paleomagnetic studies of the Velvet Room have found that the upper 5 levels correlate to the present normal polarity while the majority of the lower levels were deposited during the Matuyama reversed polarity chron (B. Raynolds and J. Friedman personal communication) and are therefore at least 0.78 million years in age. Mark's Sink, an isolated section of the Velvet Room, contains bioturbated material in its upper sections, while its lower portions are stratified and apparently undisturbed. These lower levels are also yielding mammal species, such as *Hypolagus*, that are older than those found anywhere else in the cave. Although other rooms with fossilized remains exist and have been sampled, the 3 rooms described above have produced most fossil specimens to date and may, collectively, span more than one million years.

In the 1980s certain specimens from the Pit were identified as *Brachylagus idahoensis* by Barnosky and Rasmussen (1988). While analyzing the leporid remains from the Velvet Room and Mark's Sink, I discovered several teeth and mandibles similar in size to those of *B. idahoensis* but lacking the diagnostic p3 enamel pattern of this species. When I reexamined the Pit specimens, I found that they too lacked the *B. idahoensis* form of p3. Previous morphometric work (Ramos in press) provided a large sample of extant *B. idahoensis* (*n* = 85) as well as an understanding of variation in dental characters for this species. When used for comparison with the Porcupine Cave fossils, these data demonstrated that although the fossils were similar in several ways to *B.*

idahoensis, distinct differences indicated a new species of *Brachylagus*.

METHODS

Porcupine Cave is located at 2900 m in the NW1/4 of SW1/4 Sec. 23, T15S, R76W in Park County, Colorado. Fossil material was collected by Denver Museum of Natural History (DMNH) crews using 0.64-m^2 grid excavated in 2-cm levels for the stratified deposits of the Velvet Room. The upper region of Mark's Sink is unstratified and the grid system was not applied; however, the lower sections separate into strata that have been carefully excavated utilizing the grid and level system described above. Material was screened and washed, then brought to DMNH for identification and cataloging. Material from the Pit was excavated using different methodology (see Barnosky and Rasmussen 1988) and much of that material is housed in CM.

Using Mitutoyu calipers calibrated to 0.02 mm, I measured the fossil material as well as 85 recent skulls of *Brachylagus idahoensis* for comparison. Measurements followed previously published conventions (Bensley 1926, Findley et al. 1975, White 1987) and are as follows: (1) depth of mandible at anterior alveolus of p4, (2) length of alveolar tooth row of mandible, (3) length of p3, (4) width of p3, (5) width of p4, (6) width of m1, (7) width of m2, (8) width of m3, (9) length of diastema, (10) length of maxillary alveolar tooth row, (11) depth of anterior zygomatic process, (12) width of P2, (13) width of P3, (14) width of P4, (15) width of M1, (16) width of M2, (17) width of M3. Diastemata of maxillae are rarely preserved and were not included in the analysis. Enamel pattern terminology follows White (1987, fig. 3).

The data were then subjected to descriptive statistics using Microsoft Excel. In addition, a 2-sample *t* test was performed upon widths and lengths of p3 between the 2 species. Only adult specimens of both the recent and fossil material were used. Fossil specimens were determined to be adult if the cheek teeth showed no alteration in size and enamel pattern from their base to their occlusal surface, sutures were well knit, and the bone was not highly porous. Specimens were determined to be immature and excluded from the analysis if any of the above conditions were not met.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order LAGOMORPHA Brandt, 1855
Family LEPORIDAE
Fischer de Waldheim, 1817
Genus *Brachylagus* Miller, 1900
Brachylagus coloradoensis,
new species

HOLOTYPE.—DMNH #33261, incomplete right dentary with p3; lacking incisor, p4, m1, m2, and m3, coronoid process, condyloid process, and angle of mandible (Fig. 2).

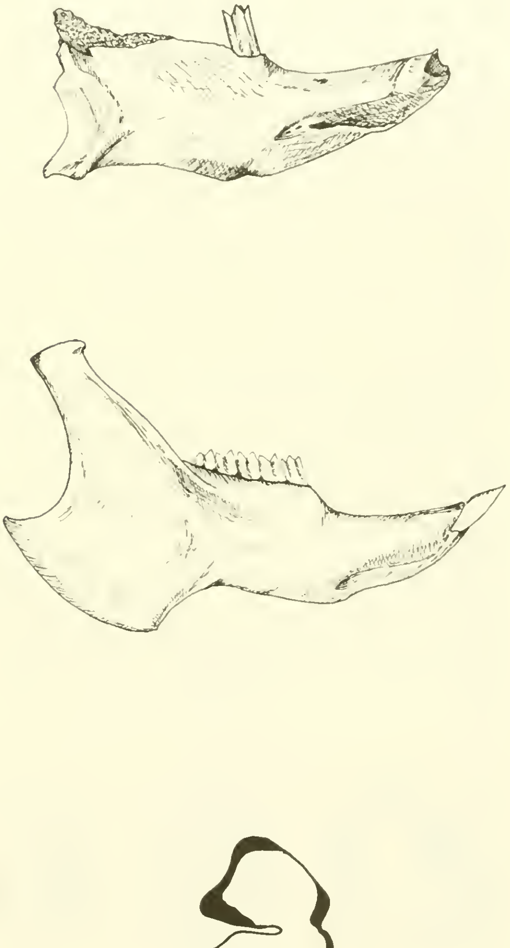

Fig. 2. DMNH #33261, holotype for *B. coloradoensis* (top), and mandible of *Brachylagus idahoensis* (UCM #5840), both shown from labial view. Camera lucida drawing of p3 from holotype; labial is to left, lingual to the right, top is anterior, bottom is posterior.

Hypodigm.—Pit: CM #66408–66409, p3; CM #66431, edentulous right maxilla; CM #66432, edentulous left maxilla; CM #65486, left dentary with p4–m2; CM #66604, p3; CM #65607, p3. Velvet Room: DMNH #28901, 33250, 33255, p3. Mark's Sink: DMNH #28902, left humerus; DMNH #33257, left dentary with p3–p4; DMNH #33260, three isolated p3s; DMNH #33272, four isolated p3s; DMNH #33271, left dentary with p3–m2; DMNH #33270, left dentary with p3–m1.

Type locality and age.—Middle Pleistocene, early to middle Irvingtonian, DMNH Locality No. 1349, Porcupine Cave, 2900 m, Park Co., Colorado (NW1/4 of SW1/4 Sec. 23, T15S, R76W, Lat. 38°43′45″N, Long. 105° 51′41″W, Gribbles Park 7.5′ Quad).

Etymology.—Named for the locality and following the precedent set in this genus. At present, this species is known only from a single site in Colorado.

Diagnosis.—The enamel pattern of the p3 is distinct from that of *B. idahoensis* in having a posteroexternal reentrant (PER) that extends between 1/3 and 2/3 the width of the tooth (Fig. 3). The posterointernal reentrant (PIR), when present, is only a slight indentation. Dimensions of postcranial material strongly resemble those of modern *B. idahoensis* but are slightly more robust.

Comparisons.—*Brachylagus coloradoensis* may be distinguished from *Hypolagus* species by its smaller size. Also, the PER of *B. coloradoensis* p3 extends farther across the tooth width, generally greater than 1/2 the distance (Fig. 3). Although *B. idahoensis* is of similar size, *B. coloradoensis*, sp. nov., is generally more robust. In comparing the size of p3, *B. coloradoensis* is approximately 12–15% larger than the average *B. idahoensis* although some specimens fall within the range of individual variation for *B. idahoensis* (Tables 1, 2). Results of the 2-sample *t* test indicate that p3 of *B. idahoensis* and p3 of *B. coloradoensis* differ in length ($F_{81,19} = 4.5$, $P < 0.0001$) and width ($F_{81,19} = 2.66$, $P < 0.001$). These results, and the differences between enamel patterns, indicate that the 2 samples are not drawn from the same population and support the designation of *B. coloradoensis* as a species separate from *B. idahoensis*. The PER of *B. coloradoensis* does not extend completely across the tooth width as in *B. idahoensis*. No complete skulls of *B. coloradoensis* are known from this site; however, portions of dentaries and edentulous maxillae are present. Disarticulated postcranial material has been tentatively assigned to this species due to the unusually small size which allows no other confident identification within the Leporidae. Several uncataloged humeri, ulnae, and podial remains have thus been identified to *B. coloradoensis* and are similar in size to corresponding elements of *B. idahoensis*.

Discussion

Brachylagus coloradoensis, sp. nov., shows some affinity to the extinct genus *Hypolagus* that radiated profusely in the Pliocene (Fig. 3). Although some p3s of *B. coloradoensis* display patterns with clear PIRs as seen in *Alilepus*, none of the upper molars found and ascribed to *B. coloradoensis* display the characteristic enamel lake found in *Alilepus*. This lake is also absent in *Hypolagus*. *Hypolagus* is easily distinguished by its simpler p3 enamel patterns and larger size.

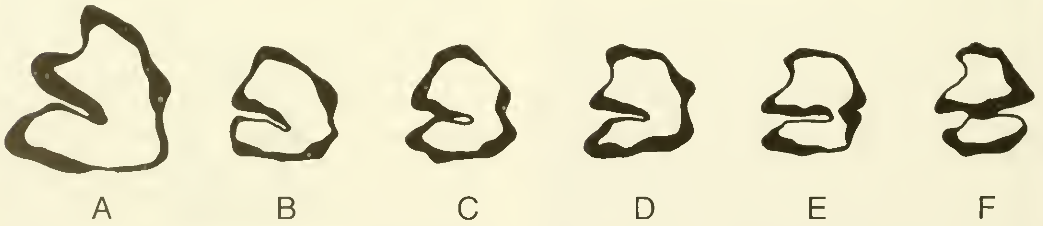

Fig. 3. Comparison of p3 enamel patterns for *Hypolagus*, *B. coloradoensis*, and *B. idahoensis*. A is *Hypolagus* (redrawn from White 1987:439), B–E (DMNH # unknown, DMNH #33257, DMNH #33255, and DMNH #33260) represent the range of variation seen in specimens of *B. coloradoensis*. B predominates slightly in earlier sediments whereas C becomes somewhat more plentiful in younger sediments at Porcupine Cave. F is that of *B. idahoensis* (UCM #5840). Note also that some specimens of *B. coloradoensis* have a slight posterior-internal reentrant (PIR).

TABLE 1. Dimensions and descriptive statistics of dentary and lower dentition of *Brachylagus coloradoensis* and *B. idahoensis* (in parentheses). Values for *B. idahoensis* are for left measurements only.

Measurement	$\bar{x} \pm s$	Range	n
Alveolar length of toothrow	10.48 (n/a)	n/a	2
	(9.1 ± 0.34)	(8.24–10.26)	(85)
Length of diastema	10.9 (n/a)	n/a	1
	(9.0 ± 0.43)	(8.46–11.92)	(85)
Depth of dentary at p4	8.86 ± 0.30	7.74–9.56	4
	(7.54 ± 0.42)	(6.60–8.26)	(85)
Length of p3	2.02 ± 0.28	1.74–2.56	19
	(1.78 ± 0.11)	(1.62–2.28)	(85)
Width of p3	1.80 ± 0.22	1.40–2.12	19
	(1.6 ± 0.11)	(1.42–2.18)	(85)
Width of p4	2.34 ± 0.12	2.12–2.54	5
	(1.96 ± 0.1)	(1.68–2.22)	(85)
Width of m1	2.35 ± 0.12	2.24–2.46	4
	(1.98 ± 0.1)	(1.78–2.26)	(85)
Width of m2	2.22 ± 0.16	2.08–2.40	3
	(1.94 ± 0.1)	(1.74–2.20)	(85)
Width of m3	1.70 (n/a)	n/a	2
	(1.02 ± 0.09)	(0.82–1.30)	(85)

TABLE 2. Dimensions and descriptive statistics of maxilla and upper dentition of *Brachylagus coloradoensis* and *B. idahoensis* (in parentheses). Values for *B. idahoensis* are for left measurements only.

Measurement	$\bar{x} \pm s$	Range	n
Alveolar length of toothrow	10.08 (n/a)	n/a	2
	(9.13 ± 0.35)	(8.32–10.1)	(85)
Depth of zygomatic process	3.49 (n/a)	n/a	2
	(3.49 ± 0.31)	(2.88–4.24)	(85)
Width of P2	2.09 (n/a)	n/a	2
	(1.73 ± 0.14)	(1.52–2.36)	(85)
Width of P3	3.19 (n/a)	n/a	2
	(2.96 ± 0.2)	(2.58–3.38)	(85)
Width of P4	3.19 (n/a)	n/a	2
	(2.98 ± 0.17)	(2.52–3.64)	(85)
Width of M1	3.05 (n/a)	n/a	2
	(2.87 ± 0.18)	(2.36–3.26)	(85)
Width of M2	2.6 (n/a)	n/a	2
	(2.6 ± 0.15)	(2.32–2.96)	(85)
Width of M3	1.15 (n/a)	n/a	2
	(1.07 ± 0.18)	(0.6–1.84)	(85)

The lower third premolar (p3) is considered somewhat diagnostic among leporids and has been used in numerous species descriptions, especially of extinct leporids (White 1984, 1987, 1991a, 1991b, Hibbard 1963). In *B. coloradoensis* there is some variation in this character which, based upon the limited number of specimens available, seems to be present regardless of geologic age. In short, no particular evolutionary trend is seen in this character. Although the simplest form is slightly more prevalent in older strata and the more derived form seems more prevalent in later strata, both extremes of the continuum are present in oldest and youngest strata. The range of variation in the p3 enamel pattern of *B. coloradoensis* is depicted in Figure 3. The P2 contains a single anterior reentrant as in *B. idahoensis* and *Hypolagus.*

The size of the Mark's Sink *B. coloradoensis*, which is presumably the oldest in the cave, is somewhat larger than that of either the Velvet Room or Pit specimens of *B. coloradoensis* (Fig. 4) while retaining more conservative p3 enamel patterns. This is an intriguing trend and may indicate a time frame for the cladogenic event that gave rise to the genus *Brachylagus.* Unfortunately, the strata from which these earliest specimens come are bracketed only with upper and lower time limits and there is little refinement in the age estimates of the levels themselves. Therefore, a more accurate picture of the rate at which the variation narrowed is not possible at this time.

However, the wide range of size variation noted for specimens of *B. coloradoensis* in the early Irvingtonian of Porcupine Cave (Fig. 4) may indicate that the cladogenetic event occurred shortly (in geologic terms) before the Porcupine Cave record. At least 2 species of *Hypolagus,* as yet unidentified, are present in the older sections of Mark's Sink with the *B. coloradoensis* material. One of these species is very small, though still somewhat larger than the largest specimens of *B. coloradoensis.* The relationship between *B. coloradoensis* and this small *Hypolagus* is unclear at present. A more detailed phylogenetic analysis utilizing several characters is currently in progress and should provide stronger evidence concerning the origins of *Brachylagus* and its relationships to extinct and extant genera (C.N. Ramos in preparation).

Of the hypotheses concerning the ancestral stock of this genus (Fig. 1), it appears just as likely that *Brachylagus* arose directly from *Hypolagus* as from *Alilepus.* Although *B. coloradoensis* exhibits p3s of both *Hypolagus* and *Alilepus* form, there are no enamel lakes present in any of the upper molars examined. Enamel lakes in upper cheek teeth are absent in *Hypolagus,* but present in P3 of *Alilepus,* and may represent plesiomorphic characters retained from Paleolaginae from which Archaeolaginae arose. Also, the time frames hypothesized by Hibbard (1963) and White (1991a) are unsubstantiated by the fossil record as there is no evidence that *Brachylagus* existed earlier than the very latest Blancan to earliest Irvingtonian.

Genera such as *Lepus* and *Sylvilagus* are not considered to have originated directly from *Hypolagus.* One or more potential intermediates have been hypothesized over the years, including *Alilepus, Serengetilagus (Pliopentalagus),* and others (Hibbard 1963, White 1991b), and fossil evidence does not dispute these hypotheses. However, *B. coloradoensis* appears to indicate a more direct transition from *Hypolagus* to *Brachylagus.* Thus, the living pygmy rabbit may be the only direct descendent of an extinct genus and may be more distantly related to *Sylvilagus* than previously thought. Although Halanych and Robinson (1997) found some molecular evidence placing *Brachylagus* as sister taxon to *Sylvilagus* based upon mitochondrial 12S rDNA data, other aspects of their analysis did not support this strongly. I find that the high degree of morphological differences between *Brachylagus* and *Sylvilagus,* as well as the paleontological evidence described above, present a strong case against a close relationship between them (see also Kenner 1965, Green and Flinders 1980).

Given the high degree of habitat specificity exhibited by the extant species of *Brachylagus,* it would be interesting to determine whether its extinct species was also highly habitat specific. Unfortunately, paleoecological evidence at Porcupine Cave is scanty and restricted mostly to faunal remains. Such postcranial remains as have been assigned to *B. coloradoensis* resemble *B. idahoensis* in almost all details. This indicates a similar degree of locomotor adaptation as seen in the extant species. *Brachylagus coloradoensis* was probably also closely

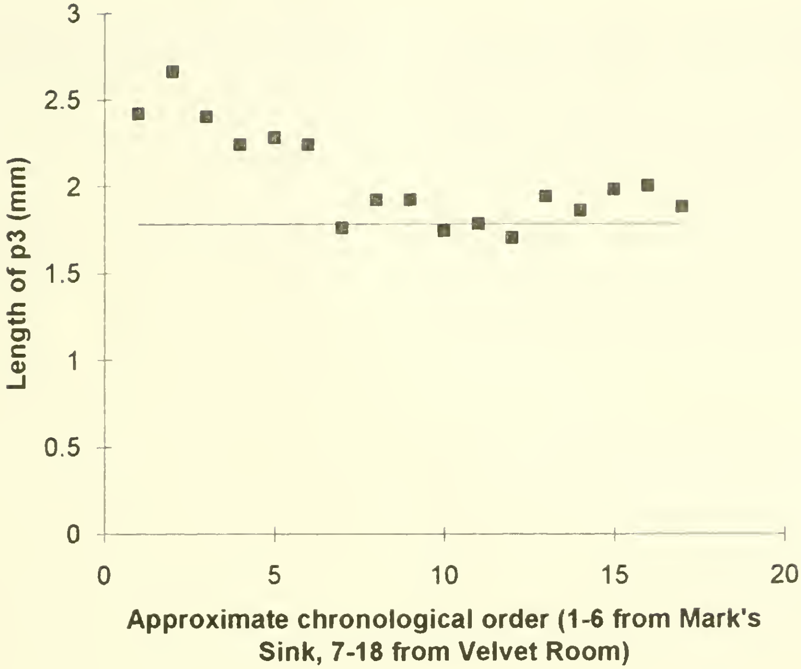

Fig. 4. Change in p3 length over time. Size data plotted over time for the different rooms in Porcupine Cave. Length of p3 has been used to illustrate the general trend, that of wide size range in older sediments, then loss of upper size limits and closer approximation to size range of *B. idahoensis*. Line indicates average p3 length for *B. idahoensis*.

allied to brush and dense cover and avoided open areas, although the plant biota comprising its habitat is impossible to ascertain at this time. However, Barnosky and Rasmussen (1988) reported the consistent concurrence of sage vole (*Lagurus curtatus*) with *B. coloradoensis* (reported as *Sylvilagus idahoensis*). This arvicoline rodent is generally found in stands of *Artemisia* (Armstrong 1972) and currently has a distribution overlapping that of *B. idahoensis*. Both mammal species are absent from the Wyoming Basin, as is *B. idahoensis*, despite the apparent presence of suitable habitat (Walker 1987). The presence of an Irvingtonian species of *Brachylagus* on the eastern side of the Continental Divide and the persistence of extant *Brachylagus* in the Great Basin may indicate that the 2 populations became isolated on opposite sides of the Rocky Mountains after dispersing through the Wyoming Basin. Where the genus originated is unclear; and although I find the presence of a small *Hypolagus* associated with *B. coloradoensis* in the older strata of Mark's Sink to be suggestive, it certainly is not conclusive.

Although complete species associations cannot be reconstructed at this time for Porcupine Cave, it is notable that this new species of leporid was associated with extinct leporids such as *Aztlanolagus* and *Hypolagus* in the oldest sections of Porcupine Cave, yet found with extant species such as *Lepus townsendii* and *Sylvilagus audubonii* in younger sediments at this site (Ramos 1998). These associations do not necessarily indicate sympatry but do indicate a temporal coexistence. Sympatry is rare among species of rabbits and hares, and the remains at Porcupine Cave are the result of predation by raptors and mammals, some of which have large ranges. Prey remains are thus sampled from a potentially wide radius and do not represent close species associations. It is still intriguing to find that this little leporid was able to survive while other leporid species, even genera, were going extinct. Unfortunately, the fossil record at Porcupine Cave truncates several hundred thousand years ago and we cannot know, at this time, how long *B. coloradoensis* survived in association with modern fauna.

Porcupine Cave is continuing to be excavated and specimens of this new species are being added to the collections at DMNH. In addition, temporal limits of localities within the cave are being clarified, which will allow more refined analysis of morphological change, speciation rate, and faunal associations. As further analysis of this important Irvingtonian site continues, our understanding of this extinct species will continue to grow, hopefully providing new insights into the evolutionary history of the single living species of *Brachylagus*.

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David Daitch of the University of Colorado at Boulder provided the excellent drawings for the figures. I also thank the following individuals for their help with this work: Cheri A. Jones and the Denver Museum of Natural History; Dave Armstrong of the University of Colorado at Boulder; Elaine Anderson, Russ Graham, Kathy Honda, and Kirk Johnson of the Denver Museum of Natural History; Jane Bock, Herbert Covert, Carol Wessman, Greg Carey, and Jill Skarstad of the University of Colorado at Boulder; Christopher J. Bell, Anthony D. Barnosky, Julio Friedman, C.A. Repenning, Bob Raynolds, Don and Jerry Rasmussen, Lou Taylor, and all the Porcupine Cave volunteers. Thanks to the following institutions for the generous use of specimens: Denver Museum of Natural History, Carnegie Museum of Natural History, Idaho Museum of Natural History, Field Museum, National Museum of Natural History, University of Colorado Museum, and Cowan Vertebrate Museum. William Akerston, Anthony D. Barnosky, and John White acted as reviewers and their comments helped improve the original draft.

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A NEW SPECIES AND NEW SYNONYM IN THE GENUS *PSYCHORONIA* (LIMNEPHILIDAE), WITH SIGNIFICANT RECORDS FOR CADDISFLIES (TRICHOPTERA) FROM WESTERN NORTH AMERICA

David E. Ruiter[1]

ABSTRACT.—A new species of caddisfly, *Psychoronia brooksi* (Limnephilidae), is described from New Mexico, and *Psychoronia brevipennis* (Banks) 1904 is designated as a junior synonym of *Psychoronia costalis* Banks 1901. Additional distributional records and notes for 51 caddisfly species are also presented.

Key words: Trichoptera, caddisflies, Limnephilidae, Psychoronia, *new species, biogeography.*

The discovery of a new species of *Psychoronia* in New Mexico has led to a review of the other 2 species in the genus and a resultant synonymy. Additional work at small, isolated habitats in the arid West will undoubtedly result in the discovery of additional new species of Trichoptera. These isolated distributions also emphasize the need to protect such habitats whenever possible.

Two species previously have been placed in the genus *Psychoronia*, *P. brevipennis* (Banks 1904) and *P. costalis* (Banks 1901). Wiggins (1975) provided rationale for maintaining the genus *Psychoronia* and figured the adults of *P. costalis*. Wiggins (1975) also noted the similarity of the 2 species and illustrated the larvae of *P. costalis* (Wiggins 1977). *Psychoronia brevipennis* is known only from the female holotype. During preparation for this paper I attempted to collect at/near the New Mexico type localities for both *P. brevipennis* and *P. costalis*. The top of the Las Vegas Range (the type locality of *P. costalis*) is located west of Las Vegas, New Mexico, and just west of Beulah. The type locality of *P. brevipennis* is also located west of Las Vegas near the former townsite of Beulah (2438 m). I could not locate populations of *Psychoronia* at or near the Beulah townsite. Based on discussions with residents in the area and the condition of existing aquatic habitats, it appears that many typical *P. costalis* habitats (headwater springs and very small streams) were altered/destroyed to create water supplies for recreational homes being built in the area.

Based on examination of the lectotype and paratype males in the type series of *P. costalis* (MCZ #11676), the single female holotype of *P. brevipennis* (MCZ #11657), and numerous series of *P. costalis* specimens from Colorado, *P. brevipennis*, as Wiggins (1975) suggested, is a new junior synonym of *costalis*. The holotype female of *P. brevipennis* is small (about 8 mm from head to apex of abdomen) when compared to female specimens of *P. costalis* from Colorado (up to 14 mm total length). However, terminalia of the *P. brevipennis* holotype are well within the variability seen in *P. costalis* females. Banks' (1904) indication that the wing membrane of *P. brevipennis* does not have hairs is in error. The membrane of the wing is clothed with strong, upright hairs as I indicated for *P. costalis* (Ruiter 1995). The wing membrane of the new species described below also has a few upright hairs, although the majority of the hairs on the membrane are fine and recumbent, similar to the genus *Hesperophylax*.

Terminology for genital structures follows that of Schmid (1980).

Psychoronia brooksi, new species

(Figs. 1–10)

The discovery of this new species occurred while I was looking for *P. brevipennis*. The occurrence of *Psychoronia* in this habitat, a small, high-velocity stream, was totally unexpected as my previous collections of *Psychoronia* had been only from headwater spring

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sources. This collection is another example of a species occurring on an isolated mountain in the southwestern United States. This species is named for Bill Brooks, a comrade with numerous interests, one of which is occasionally collecting caddisflies.

ADULT.—Wings and body yellowish brown; forewing membrane patterned, with pale areas margined with darker brown (Fig. 1), wing membrane with numerous long, upright and recumbent setae, nearly as long as those on wing veins. Wings of female extending beyond apex of abdomen, as long as wings of male. Length from front of head to end of forewings 16–18 mm. Spurs 1-3-4.

MALE (Figs. 2–4).—Tergite VIII with an apical patch of large, upright spines (in *P. costalis* this patch comprises slender, recumbent spines). Segment IX separated dorsally, with widest portion slightly above the mid-lateral line. Inferior appendages large, directed dorsocaudad. Segment X with intermediate appendages fused into triangular structure surrounding anal opening in caudal view, its dorsal apex extended into narrow, slightly bifid process (in *P. costalis* the apex of the intermediate appendages is acute and recurved). Superior appendages large, mesally concave, dorsally slightly concave with blunt apices; extending caudad nearly to apices of inferior appendages. Phallic parameres each terminated in several long, strongly sclerotized spines divided completely to base of paramere, the dorsal portion a thick, sinuous spine, curving laterad apically and apex with minute serrations along dorsal margin, the ventral aedeagal spines straight, clumped at their base (in *P. costalis* the parameres are shorter and the dorsal portion is composed of short, fused spines).

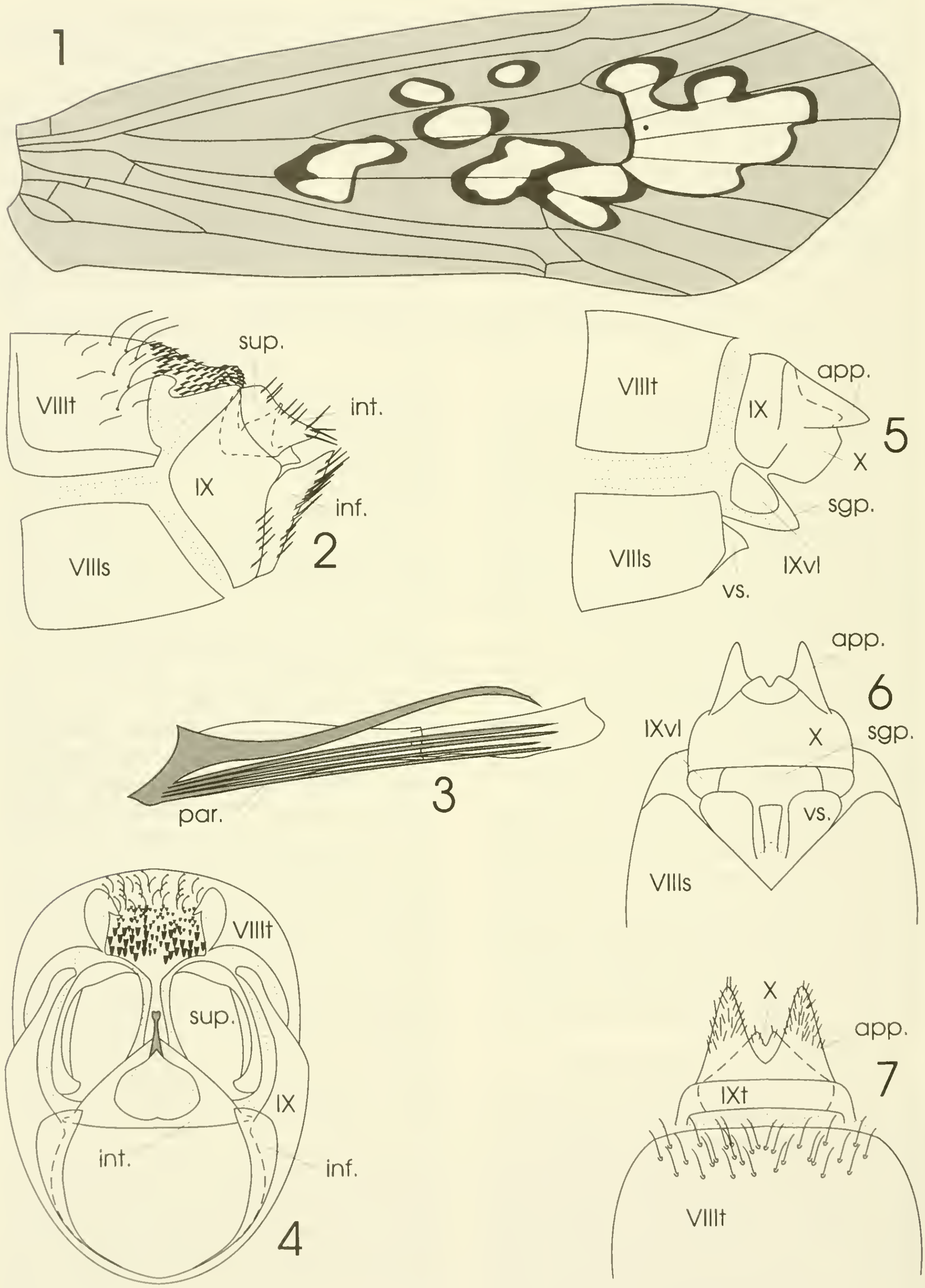
FEMALE (Figs. 5–7).—Ventromesal sclerotized spur on sternite VI absent. Abdominal sternal setae equal in thickness to tergal setae. Tergite IX bandlike, separated by faint suture from its very small ventrolateral lobes; ventrolateral lobes widely separated ventrally by broad, slightly sclerotized supragenital plate. Median lobe of vulval scale clavate, with broad, truncate apex, not extending caudad as far as apices of lateral lobes. Segment X fused to tergite IX and with apex tubular, its dorsal margin slightly cleft, its ventral margin concave, entire. Appendages of segment X located dorsolaterally, extending well beyond its apex, triangular in dorsal, ventral, and lateral views (in *P. costalis* the appendages of segment X are very short, not extending to apex of X).

LARVA (Figs. 8–10).—Most characters typical of Limnephilini (Wiggins 1977). Mandibles each with cutting edge entire, except for single subapical tooth (in *P. costalis* mandibles with numerous apical teeth). Head and thoracic sclerites dark, nearly black, with faint muscle scars on head. Primary setae absent from anterior pronotal margin (in *P. costalis* primary setae are present and equally spaced). Dorsal and ventral gills present on abdominal segments 2–7, most with 3–5 filaments; lateral gills present only on segments 2 and 3, most specimens with 2 filaments for each lateral gill. Abdominal dorsal chloride epithelia absent, ventral chloride epithelia large, present on segments 2–7.

CASES.—The larval case is made of sand grains, only slightly tapered from wide anterior end to posterior, and slightly curved. Pupal case (17–20 mm) made of larger rock particles similar to that of *P. costalis* (see Wiggins 1977, Fig. 10.46), nearly straight, not tapered. Several cases have incorporated occasional live fingernail clams.

TYPE SPECIMENS.—Holotype and allotype. NEW MEXICO: Lincoln County, North Fork Rio Ruidoso, at entrance to Ski Apache Ski Area, collected as pupae 24 May 1997, emerged 20 June 1997, D.E. Ruiter. Deposited: Museum of Comparative Zoology. Paratype males: same data, emerged 20–22 June 1997, deposited Museum of Comparative Zoology, National Museum of Natural History, Illinois Natural History Museum, Royal Ontario Museum. A paratype male and female, same data, deposited at NMNH. A pupal exuvia and 4 larvae, same data, deposited at each of the above collections. The remainder of the adult (8 males, 1 female), pupal, and larval material from the same collection retained in author's collection.

DIAGNOSIS.—Males of *P. brooksi* can be separated readily from *P. costalis* by the stiff, dark spines on tergite VIII versus the fine, hairlike spines on tergite VIII of *P. costalis*. In addition, phallic parameres of *P. brooksi* are at least twice as long as those of *P. costalis*. Females of *P. brooksi* have normal length wings that extend well beyond the abdomen, while wings of all females of *P. costalis* I have examined do not extend beyond the 8th abdominal segment and usually do not exceed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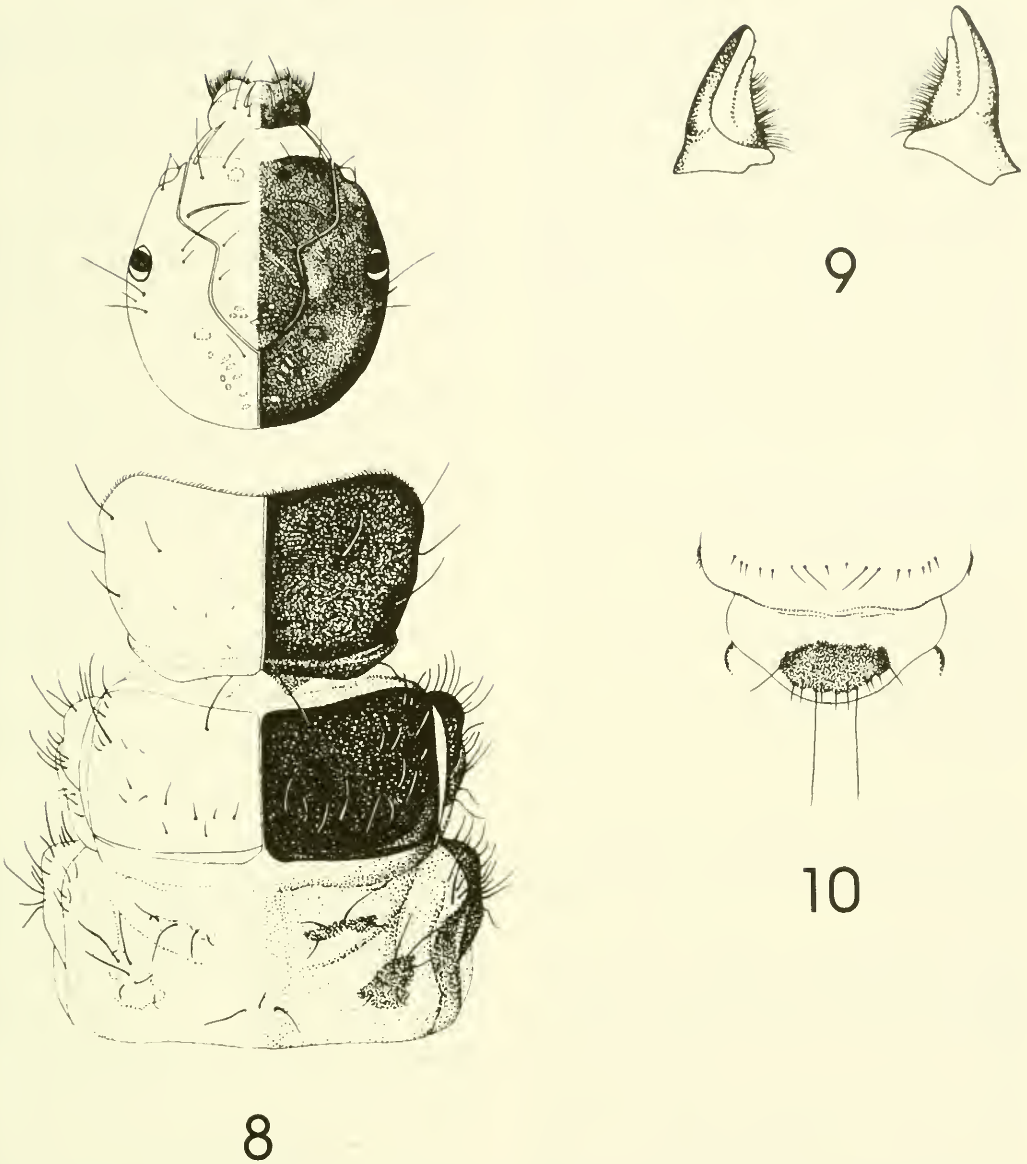
Figs. 1–7. *Psychoronia brooksi* forewing and genitalia: 1, right side forewing; 2, male genitalia, left lateral view; 3, male aedeagus, left lateral view, 4, male genitalia, caudal view; 5, female genitalia, left lateral view; 6, female genitalia, ventral view; 7, female genitalia, dorsal view (VIIIt – tergite VIII segment, VIIIs – sternite VIII segment, IXt – tergite IX segment, IXvl – ventrolateral lobe IX segment, X – X segment, app. – appendage, inf. – inferior appendage, int. – intermediate appendage, sgp. – supragenital plate, sup. – superior appendage, vs. – vulval scale).



Figs. 8–10. *Psychoronia brooksi*, larva: 8, head and thorax, dorsal view; 9, mandibles, dorsal view; 10, ninth abdominal tergite, dorsal view.

the 5th abdominal segment. Appendages of the female *P. brooksi* segment X extend posteriorly well beyond the apex of segment X, while those of *P. costalis* do not reach the apex of segment X. Larvae of the 2 species can be separated based on the setae of the pronotum: *P. costalis* has several evenly spaced setae along the anterior margin of the pronotum (see Wiggins 1977, Fig. 10.46), whereas these setae are absent in *P. brooksi*.

REMARKS.—The occurrence of a macropterous female *Psychoronia* conflicts with the primary character Banks (1916) used to define the genus: "female short-winged." Wiggins (1977) separated *Psychoronia* larvae from *Hesperophylax* based on the lack of lateral gills beyond segment 3 in *Psychoronia*. This character seems to be valid for *P. brooksi*, although *P. brooksi* larvae usually have the posterior lateral gill branched. I have also seen occasional

Colorado *P. costalis* larvae with branched lateral gills. Another character that appears to separate *Psychoronia* larvae from *Hesperophylax* is the reduced number of primary setae along the anterior pronotal margin of *Psychoronia*. In *Hesperophylax* the primary setae are numerous and not evenly spaced.

Psychoronia brooksi is known only from the type collection, which consisted of numerous larvae and pupae. Adults were reared from pupae by placing the pupae in plastic bags along with a piece of damp moss. The bags were transported in a cooler on ice for about a week and then placed in a home refrigerator. Adults started emerging in the refrigerator about a month later. Larvae were numerous throughout all but the highest velocity habitats of the North Fork Rio Ruidoso. This flowing-water habitat, along with the scraper mandibles of the larvae, is unusual for most members of the Limnephilini, but similar to that of *Hesperophylax*. The stream had a maximum width of about 2.5 m at the time of collection. Pupae were located in aggregations of 5 to 10 along the lateral margins of the largest boulders I could turn over in the stream, just below the water-substrate interface. This is often the same type of habitat where *Hesperophylax* pupae are found. This is not usually the case for Colorado *P. costalis* pupae, which are often lying scattered throughout the vegetation of headwater seepage area habitats, although they may be attached to rocks and sticks. I have not seen *P. costalis* in streams larger than about 0.4 m wide; they are most often found within <3 m of the headwater spring source. There also seems to be some type of habitat partitioning between *P. costalis* and *Hesperophylax*. Whereas *Hesperophylax occidentalis* (Banks) is very common in high-altitude Colorado headwater seepage areas, in those seepage areas which contain *P. costalis*, *H. occidentalis* is found further downstream in the outlet stream. A single *Hesperophylax* sp. larva (along with larvae of *Lepidostoma* sp. and *Oligophlebodes* sp.) was collected along with the *P. brooksi* larvae.

The presence of 10-mm larval cases and 20-mm pupal cases in late May suggests a 2-yr life cycle for *P. brooksi*. In Colorado *P. costalis* emerges from late July through early September, and I have not seen evidence of small larvae being present during emergence, therefore suggesting a univoltine life cycle for *P. costalis*.

ADDITIONAL RECORDS AND NOTES ON WESTERN NORTH AMERICAN CADDISFLIES

The following are additional distributional records for western North American caddisflies. Special recognition goes to the following institutions/individuals for providing most of these specimens: Colorado State University, C.P. Gillette Museum of Arthropod Diversity, B.C. Kondratieff (CSU); University of Wyoming, R.J. Lavigne (UW); Purdue University, A. Provonsha (PU); Brigham Young University, Monte L. Bean Life Science Museum, R.W. Baumann (BYU); Illinois Natural History Survey, K.A. Methven (INHS); California Academy of Sciences, V.F. Lee (CAS); Dean Blinn (DB); G.Z. Jacobi (GZJ); and S.R. Moulton II (SRM).

Apataniidae

Apatania shoshone Banks 1924. ALASKA: Katmai Peninsula; at lights, Alaknak River, Alaknak Lodge, W.G. Downs, 22 August 1987, 2M 1F (DER).

Apatania zonella (Zetterstedt) 1840. WYOMING: Albany County, Meadow Creek at Glacier Lakes, Medicine Bow National Forest, H. Copeland, 29 June 1987, 1F; West Glacier Lake, Medicine Bow National Forest, B.C. Kondratieff & W.B. Painter, 21 July 1987, 1F; Glacier Lakes, T. Ebert, 4 July 1988, 3F (CSU); Carbon County, swept from herbage near edge of Lake Marie, 20 km W of Centennial, P.H. Arnaud, Jr., 1 August 1973, 1F (CAS).

Brachycentridae

Micrasema onisca Ross 1947. ARIZONA: Coconino County, front passage to Roaring Springs Cave, Grand Canyon National Park, D. Blinn, 28 September 1994, 1M 1F (DB).

Glossosomatidae

Agapetus boulderensis Milne 1936. NEW MEXICO: Colfax County, creek, U.S. 64, west of Cimmarron, M. Harris, 8 August 1990, 11M 1F (CSU).

Glossosoma velonum Ross 1938. YUKON TERRITORY: Stewart River at Mayo, J.C. Abbott & K.W. Stewart, 24 June 1996, 1F; Ross River, at Canol Road, 2.1 mi N of Perry Barge, J.C. Abbott & K.W. Stewart, 25 June 1996, 3M 7F (SRM).

Protoptila coloma Ross 1941. Wyoming: Park County, Firehole River, near Old Faithful, B.C. Kondratieff, 8 June 1987, 15M (CSU); Teton County, Gibbon River, Gibbon Falls Picnic Ground, Yellowstone National Park, R.J. Lavigne, 13 July 1989, 3M (UW).

Goeridae

Goereilla baumanni Denning 1971. Washington: Spokane County, small streams, Big Spring Picnic Ground on Mount Spokane, D.E. Ruiter, 9 June 1996, 1M (DER).

Hydropsychidae

Ceratopsyche protis (Ross) 1938. Arizona: Santa Cruz County, Santa Rita Lodge, Madera Canyon, P.A. Opler, 30 July 1991, 2M (CSU); Wyoming: Sublette County, Green River at Highway 191, K.D. Alexander & L.A. Stewart, 4 August 1995, 9M 3F (SRM).

Cheumatopsyche lasia Ross 1938. Colorado: Las Animas County, Purgatoire River, Iron Canyon, Rourke Ranch, PCMS, B.C. Kondratieff, 14 July 1991, 13M 1F; Otero County, Purgatoire River, Route 109, B.C. Kondratieff, 9 April 1992, 2M (CSU).

Hydropsyche californica Banks 1899. New Mexico: Catron County, at light, Taylor Creek below Wall Lake, Gila National Forest, B.C. Kondratieff & R. Durfee, 24 July 1994, 22M 15F; Dona Ana County, Radium Springs, H.E. Evans, 13 May 1989, 9M; Sierra County, Rio Grande, Percha Dam State Recreation Area, B.C. Kondratieff, 17 July 1989, 20M 8F (CSU).

Hydropsyche occidentalis Banks 1900. Nevada: Washoe County, Truckee River, Verdi Fish Hatchery, R.W. Baumann, 10 May 1983, 1M (BYU); South Dakota: Bennett County, 10 mi E of Martin, La Creek National Wildlife Refuge, P.A. Opler, 26 May 1990, 1M 1F; Fall River County, Hot Springs, B.C. Kondratieff, 15 July 1988, 11M (CSU).

Smicridea fasciatella McLachlan 1871. California: Riverside County, Colorado River, Route 95, B.C. Kondratieff & R.W. Baumann, 20 June 1988, 6M 1F; Colorado River, Mayflower Park, Blythe, B.C. Kondratieff & R.W. Baumann, 20 June 1988, 6M 12F (CSU).

Hydroptilidae

Agraylea saltesea Ross 1938. Wyoming: Park County, Virginia Cascades, Yellowstone National Park, H.R. Lawson, 19 July 1989, 3M 2F (CSU).

Hydroptila ajax Ross 1938. California: Riverside County, Colorado River, Route 95, B.C. Kondratieff & R.W. Baumann, 20 June 1988, 2M (CSU). This appears to be a significant western extension of records for this species.

Hydroptila angusta Ross 1938. Wyoming: Crook County, Belle Fourche River, Hulett, B.C. Kondratieff & R.W. Baumann, 15 July 1997, 1M (CSU). This extends the distribution of this species further northwest.

Hydroptila arctia Ross 1938. New Mexico: Grant County, West Fork of Gila River, at Road 15, Gila National Forest, P. McCafferty, A. Provonsha, & D. Bloodgood, 6 May 1981, 1M 5F (PU).

Hydroptila consimilis Morton 1905. North Dakota: Hettinger County, Cannonball River, New England Route 22, B.C. Kondratieff & R.W. Baumann, 15 July 1997, 4M 4F (CSU).

Hydroptila pecos Ross 1941. Montana: Bighorn County, Bighorn River, Fort Smith, D.E. Ruiter, 5 September 1991, 17M (DER); South Dakota: Fall River County, Fall River, Hot Springs, B.C. Kondratieff, 15 July 1988, 2M 1F; 5 February 1995, 2M 1F (CSU).

Hydroptila salmo Ross 1941. Wyoming: Carbon County, Medicine Bow River, about 2 mi E of Elk Mountain on Interstate 80, R.J. Lavigne, 23 August 1982, 5M (UW).

Leucotrichia pictipes (Banks) 1911. South Dakota: Fall River County, Fall River, Hot Springs, B.C. Kondratieff, 15 July 1988, 10M 4F; 5 February 1995, 6M 1F (CSU).

Ochrotrichia alsea Denning & Blickle 1972. California: Butte County, Diamond Timber, 2.5 mi E of Hwy 52 and Rd 150G, P.A. Opler & E. Buckner, 9 July 1993, 5M (CSU).

Ochrotrichia logana Ross 1941. Alaska: Katmai Peninsula, at lights, Alaknak River, Alaknak Lodge, W.G. Downs, 22 August 1987, 1M 2F (DER). This represents a major northwestern distribution extension.

Ochrotrichia stylata (Ross) 1938. New Mexico: Grant County, West Fork of Gila River, at Rd 15, Gila National Forest, P. McCafferty, A. Provonsha, & D. Bloodgood, 6 May 1981, 1M (PU).

Ochrotrichia tarsalis (Hagen) 1861. South Dakota: Fall River County, Fall River, Hot Springs, B.C. Kondratieff & R.W. Baumann, 5 February 1995, 3M 4F (CSU).

Orthotrichia aegerfasciella (Chambers) 1873. COLORADO: Larimer County, black light trap, Mail Creek, P.A. Opler, 18 August 1988, 1F; 10 August 1989, 2M (CSU). This appears to be the westernmost collection for this species.

Oxyethira pallida (Banks) 1904. COLORADO: Baca County, East Carrizo Creek, Carrizo Creek Picnic Ground, B.C. Kondratieff, 16 July 1992, 1M; Larimer County, light trap, Mail Creek, Fort Collins, P.A. Opler, 29 August 1989, 1M; black light trap, Shields Pond, off Shields Road, B.C. Kondratieff, 5 July 1991, 24M 15F; black light trap, Shields Pond, Fort Collins, B.C. Kondratieff & R. Durfee, 5 July 1991, 22M 30F; Montezuma County, Toten Reservoir, east of Cortez, B.C. Kondratieff, 2 May 1992, 10M 4F (CSU).

Zumatrichia notosa (Ross) 1944. NEW MEXICO: Grant County, West Fork of Gila River, at Rd 15, Gila National Forest, P. McCafferty, A. Provonsha, & D. Bloodgood, 6 May 1981, 4M 2F (PU).

Lepidostomatidae

Lepidostoma apornum Denning 1949. ARIZONA: Coconino County, front passage to Roaring Springs Cave, Grand Canyon National Park, D. Blinn, 28 September 1994, 1M (DB); COLORADO: Larimer County, Upper Beaver Meadows Picnic Area, Rocky Mountain National Park, P.A. Opler, 12 July 1990, 2M (CSU); Laramie River, at Honholtz Lakes access, D.E. Ruiter, 15 July 1988, 9M 3F (DER).

Lepidostoma cascadense (Milne) 1936. NEW MEXICO: Taos County, Red River at Zwergel Dam, G.Z. Jacobi, 29 July 1980, 1M (GZJ).

Leptoceridae

Ceraclea annulicornis (Stephens) 1836. WYOMING: Carbon County, Big Creek, 3 mi above confluence with North Platte River, D. Rees, 27 June 1988, 3M 3F (CSU); Park County, Slough Creek Campground, Yellowstone National Park, R.J. Lavigne, 2 August 1990, 2M 2F (UW).

Oecetis cineraxcens (Hagen) 1861. COLORADO: Baca County, Picture Canyon, B.C. Kondratieff, 15 June 1994, 1M (CSU).

Oecetis immobilis (Hagen) 1861. COLORADO: Saguache County, at lights, Russell Lakes State Wildlife Area, R. Durfee, 6 July 1994, 3M; 17 July 1994, 1M 3F; 8 August 1994, 2M 8F (CSU). These appear to be the southwesternmost records for this species.

Oecetis inconspicua (Walker) 1852. NEW MEXICO: San Miguel County, Pecos River, near Monastery Lake, G.Z. Jacobi, 5 October 1980, 1M (CSU).

Triaenodes tardus Milne 1934. CALIFORNIA: Butte County, 10 mi ESE of Chico, Centerville, P.A. Opler, 11 August 1993, 2M 1F (CSU).

Limnephilidae

Asynarchus circopa (Ross & Merkley) 1952. WYOMING: Big Horn County, Meadowlark Lake, Bighorn National Forest, M.W. Sanderson, 24 August 1954, 1M (INHS); Fremont County, Golden Lakes, Middle Fork Bull Lake Creek, D. Rees, 6 August 1996, 2M (CSU); Teton County, Lewis Lake, Yellowstone National Park, R.J. Lavigne, 31 July 1990, 1M (UW).

Asynarchus montanus (Banks) 1907. Herrmann et al. (1986) did not report this species from Colorado, doubting the record of Schmid 1955. I have now seen specimens from the west side of Rocky Mountain National Park. COLORADO: Grand County, 1.2 mi S of Bowsu Baker Trailhead, Rocky Mountain National Park, P.A. Opler, 23 July 1994, 1M; Harbison Picnic Area, Rocky Mountain National Park, P.A. Opler & E. Buckner, 29 July 1995, 1M; Green Mountain Employee Area, Rocky Mountain National Park, P.A. Opler, 30 August 1997, 1M (CSU); OREGON: Clatsop County, black light trap, Astoria, K. Goeden, 1 September 1969, 1M (CAS).

Asynarchus mutatus (Hagen) 1861. UTAH: Duchesne County, White Rocks River below Chepeta Lake, Ashley National Forest, R.C. Mower, 20 July 1984, 1M; Summit County, China Meadows, Uinta Mountains, R.W. Baumann & B.J. Sargent, 14 July 1986, 2M (BYU). These collections represent a significant southern distributional extension for this species. It seems that the Uinta Mountain area of Utah contains many interesting distributional records (see discussion under *Hydatophylax hesperus*)

Chyranda centralis (Banks) 1900. NEVADA: Elko County, stream above Angel Lake, Ruby Mountains, R.W. Baumann, 3 August 1990, 1M 1F (BYU).

Clistoronia flavicollis (Banks) 1900. WASHINGTON: Chelan County, Minotaur Creek, 10 mi W of Wenatchee Lake, site #6, in uncut timber (north and south of Rd 2728), J.R. Wood, 14 July 1976, 1M (DER). This appears to be the most southern record for this species.

Glyphopsyche irrorata (Fabricius). WASHINGTON: Kittatus County, Teanaway River, Hwy 10, 4 mi S of Cle Elum, R.W. Baumann & S.D. Smith, 6 May 1982, 1F (BYU).

Hydatophylax hesperus (Banks) 1914. UTAH: Wasatch County, Bryants Fork Creek, Strawberry Reservoir, M. Whiting, S. Wells, & L. Liu. 14 June 1989, 1M (BYU). This record is based on a 1989 collection. Subsequent to that collection the entire drainage, including the headwater springs, was rotenoned in an attempt to restore a nonnative sport fishery in a downstream reservoir. The Bryants Fork Creek locality was revisited in 1995 and 1996 and no caddisflies were located. In an effort to create/maintain a nonnative sport fishery, it is likely that isolated native aquatic species within this drainage, such as *Hydatophylax hespersus*, have been eliminated.

Limnephilus moestus Banks 1908. NEW MEXICO: Santa Fe County, Medio Creek, at Santa Fe Ranch Ski Lodge, K.D. Alexander & L.A. Stewart, 5 July 1995, 1M (SRM).

Limnephilus sansoni Banks 1918. Ruiter (1995) indicated that the Colorado record of Dodds and Hisaw (1925) was questionable and did not include *Limnephilus sansoni* from Colorado. I have now seen specimens from Grand County, Colorado, on the opposite (western) side of the Continental Divide from the locality reported by Dodds and Hisaw. Grand County, Green Mountain Employee Area, Rocky Mountain National Park, P.A. Opler, 30 August 1997, 6M 2F (CSU).

Psychoglypha prita (Milne) 1935. The record for *Psychoglypha ormiae* (Ross) 1938 from Teton County, Wyoming (Ruiter and Lavigne 1985), is an error. These specimens are *Psychoglypha prita* (Milne) 1935. Teton County, Taggert Creek, 7000 feet, H.E. Evans, 6 October 1983, 25M (CSU).

Psychoglypha schuhi Denning 1970. WYOMING: Sublette County, Lead Creek, D.E. Ruiter, 25 October 1995, 3M (DER). This appears to be only the 2nd collection reported for this species. Type locality is in Nevada.

Polycentropodidae

Cyrnellus fraternus (Banks) 1905. COLORADO: Bent County, Caddoa Creek, at Road CC, B.C. Kondratieff, 14 July 1992, 1F; black light trap, John Martin Reservoir, B.C. Kondratieff, 16 July 1992, 3M; Prowers County, Arkansas River, U.S. 50, Lamar, B.C. Kondratieff, 23 August 1996, 1M (CSU).

Polycentropus crassicornis Walker 1852. MONTANA: Rosebud County, Colstrip, quicktrap TF R2 Q33, Leetham, 20 June 1975, 1M (DER).

Psychomyia flavida Hagen 1861. ARIZONA: Coconino County, Oak Creek, along U.S. Hwy 89A north of Sedona, S.R. Moulton, 12 June 1998, 2M 2F (SRM).

Rhyacophilidae

Rhyacophila narvae Navas 1926. WYOMING: Park County, Virginia Cascades, Yellowstone National Park, H.R. Lawson, 19 July 1989, 1M 1F (CSU).

Rhyacophila pellisa Ross 1938. NEW MEXICO: Taos County, Red River at Zwergel Dam, G.Z. Jacobi, 29 July 1980, 1M (GZJ).

Uenoidae

Neophylax rickeri Milne 1935. COLORADO: Jackson County, black light trap, North Platte River at Ginger Quill Ranch, W.G. Downs, 1 September 1990, 1F (DER). This appears to be a major southeastern distributional extension for this species.

Oligophlebodes minutus (Banks) 1897. YUKON TERRITORY: Little Rancheria Creek, at Alaska Highway, J.C. Abbott & K.W. Stewart, 26 June 1996, 1M (SRM).

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EMERGENCE PATTERNS OF LARGE STONEFLIES (PLECOPTERA: *PTERONARCYS, CALINEURIA, HESPEROPERLA*) IN A MONTANA RIVER

Andrew L. Sheldon[1]

Abstract.—Emergents of *Pteronarcys californica*, *Calineuria californica*, and *Hesperoperla pacifica* were captured with replicated emergence traps at 3 sites along the banks of Rock Creek, Montana. *Pteronarcys* emergence in early June was short (88% of individuals in 6 d) and attained rates of 5 m^{-1} d^{-1} (shoreline distance) and cumulative densities up to 19 m^{-1} yr^{-1}. *Calineuria* emerged synchronously (89% in 9 d) 2 wk later at densities up to 7 m^{-1} d^{-1} and 40 m^{-1} yr^{-1}. The less numerous *Hesperoperla* (5 individual m^{-1} yr^{-1}) had a longer emergence period partially coinciding with *Calineuria*. Median males of *Pteronarcys* and *Calineuria* emerged 2–3 d before median females; protandry was not significant in *Hesperoperla*. Sex ratios were female-biased in *Pteronarcys* and *Hesperoperla* but male-biased in *Calineuria*. Size trends through emergence were very weak although females showed a greater tendency toward larger size early in emergence.

Key words: Plecoptera, phenology, emergence traps, sex ratio, size.

Emergence, the transition from the aquatic growth phase to the reproductive and dispersal activities of terrestrial/aerial adulthood, is a critical event for aquatic insects (Macan 1958, Corbet 1964, Zwick 1990). For the biologist, collection of emergents provides a census of readily identified individuals at a defined point in the life history. Thus, emergence data are essential for life history studies and are potentially useful for monitoring. Statzner and Resh (1993) synthesized a large set of emergence studies in an analysis of species richness and other properties of stream communities; this paper, however, emphasizes population biology.

In the western United States, emergences of the stoneflies *Pteronarcys californica* Newport (Pteronarcyidae), *Calineuria californica* (Banks), and *Hesperoperla pacifica* (Banks) (Perlidae) are notable for the numbers and visibility of the large, colorful, diurnally active adults. (To avoid confusion involving the *californica* epithet, I refer to these species by their generic names throughout this paper.) As "salmonflies" (*Pteronarcys*) and "golden stoneflies" (*Calineuria, Hesperoperla*), these insects are important in angling lore and literature (Leiser and Boyle 1982). The nymphal biology of these taxa is moderately well known (Stewart and Stark 1988, Freilich 1991, DeWalt and Stewart 1995) but, aside from investigations of drumming behavior (Stewart and Maketon 1991) and *Calineuria* flight behavior (Poulton and Stewart 1988), little has been written about adults since Muttkowski (1929) described emergence of *Pteronarcys* and *Hesperoperla* in the Yellowstone River.

Emergence of stoneflies has been described from sweepnet catches (Sheldon and Jewett 1967) that confound adult longevity with emergence timing, counts of exuviae (Haro et al. 1994, Alexander and Stewart 1996), and captures in traps of various designs (Kerst and Anderson 1974, Zwick 1977, Kuusela 1984, Ernst and Stewart 1985, Bagge and Hynynen 1995, Giberson and Garnett 1996). I used catches from emergence traps, designed for this project, to describe phenology, abundance, and size and sex composition of adult *Pteronarcys*, *Calineuria*, and *Hesperoperla* in Rock Creek, Montana.

Methods

Rock Creek, a noted trout stream, originates in the Anaconda Range of western Montana and flows north 110 km to its confluence with the Clark Fork River (46°43′N, 113°41′W). Three sampling stations were established: Valley

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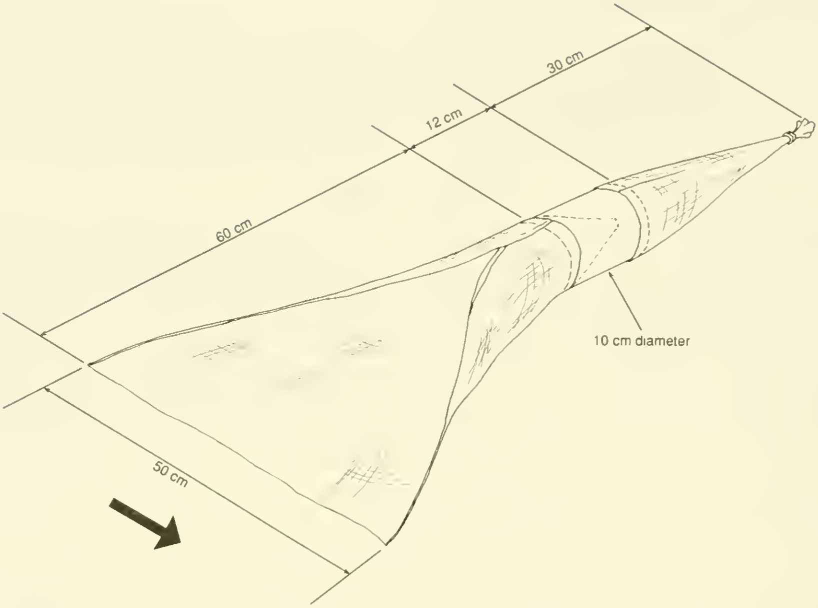

Fig. 1. Emergence trap used in this study. Arrow indicates direction of water flow along the shoreline.

of the Moon, stream km 4.0, 1095 m elevation; Ranch Creek, 20.0 km, 1207 m; Bitterroot Flat, 38.0 km, 1305 m.

The traps used (Fig. 1) were designed to intercept emerging stoneflies as they left the water. Cost was kept to a minimum since I used numerous replicates at each site and planned to sample at more sites. I also anticipated substantial trap loss from changing water levels and human interference. Traps were constructed of plastic window screen, PVC pipe, and duct tape. Each trap consisted of an apron leading upward to the PVC pipe which contained a screen funnel. Past the PVC collar, insects were captured in a stapled screen cylinder closed by a heavy rubber band which allowed easy access. Apron, funnel, and cylinder were attached to the PVC pipe with duct tape. Total cost was <\$2.00 per trap. More refined models with apron and cylinder attached by hose clamps and the funnel with epoxy resin were nearly twice as costly. However, duct tape was completely satisfactory except when the entire trap was submerged for hours.

In use, the edge of the apron was placed at or just below the water's edge and weighted with gravel and small stones. If needed, a large stone or two held the PVC pipe, and a stone at the rubber band end of the cylinder anchored the entire trap. An informational sign was placed by each trap. Traps were tended daily and moved up or down to accommodate changing water levels. Stoneflies were collected from the cylinder and also from the apron and outer surface of the funnel since, especially on cold mornings, tenerals and preecdysial nymphs sometimes failed to pass through the funnel before the traps were tended. (Nymphs were included in numbers and sex ratios but not in size data.)

At each site 20 traps were placed at 15.2-m (50-ft) intervals along one bank since the opposite shore was inaccessible at spring discharge. Identification, sex determination, and size measurement (head width, including eyes, with dissecting microscope and ocular micrometer) were done in the laboratory. Data presented here are aggregated by site; a statistical treatment of between-trap variability and precision of this and other emergence studies is in preparation.

Preliminary fieldwork in 1989, using less retentive traps without funnels, began 5 June, midway in the *Pteronarcys* emergence, and ended 13 June. In 1990 I tended traps daily 29 May–30 June. This is a period of very heavy use by anglers, so I chose not to install recording thermometers although temperature data would have been very useful.

Statistical methods follow Sokal and Rohlf (1981) and Zar (1984).

RESULTS

Emergence of these species occurs during peak spring runoff from snowmelt. Because high discharge covers rocks exposed at other seasons and limits emergence to the shoreline at the study sites, the entire emergent population was vulnerable to the traps. However, high and variable discharge washed away many traps on the gently sloping shore at the lowermost Valley of the Moon site in both years; thus, the quantitative data from that site cannot be used. One trap at Ranch Creek and, over the season, 3 at Bitterroot Flat were lost to flow and tampering. Analyses are based on data from traps persisting to the end of emergence for a particular species; i.e., $n = 19$ for *Pteronarcys* and $n = 17$ for *Calineuria* and *Hesperoperla* at Bitterroot Flat.

In 1990 very few *Pteronarcys* adults were present at Ranch Creek when traps were installed 28 May; snow and low water temperature inhibited emergence over the next few days and again on 5 June (Fig. 2). However, *Pteronarcys* emergence was extremely synchronous, with 88% of adults emerging over 6 consecutive days. The first *Hesperoperla* adults emerged with *Pteronarcys*, but the majority were contemporaneous with the abundant *Calineuria*. *Pteronarcys* and *Calineuria* peaks were separated by a week with little activity. Although *Calineuria* emergence was protracted relative to *Pteronarcys*, 89% emerged during 9 consecutive days.

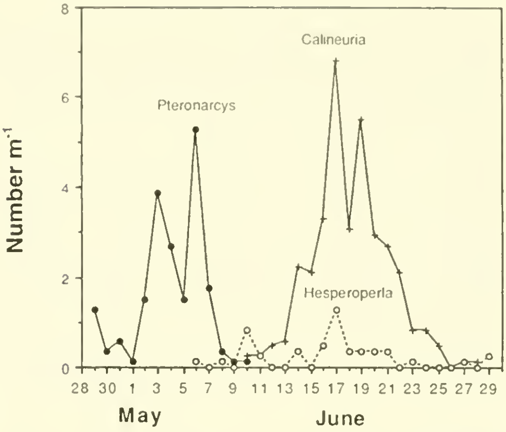

Fig. 2. Emergence (number m^{-1} d^{-1}) at Ranch Creek, 1990. (Length is shoreline length; double these number to estimate number per stream length.)

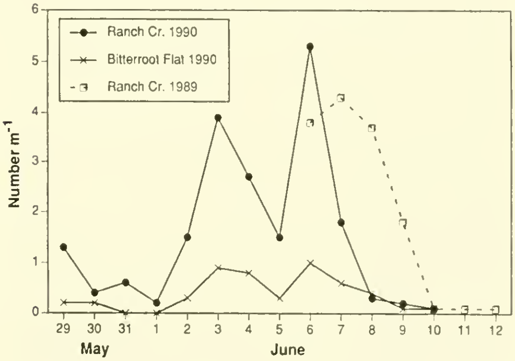

Fig. 3. Emergence of *Pteronarcys* at 2 sites in 1990 and at Ranch Creek in 1989 (no data before 6 June). Length measure is shoreline length.

Emergence timing varied within and between years (Fig. 3). *Pteronarcys* emergence in 1990 at the upper 2 sites was in phase and controlled by cold weather in late May and on 5 June. Not shown in Figure 3 are 3 exceptionally late *Pteronarcys* emergents at Bitterroot Flat (males on 16, 18 June; female 24 June). Emergence at Ranch Creek in 1989 was slightly later than in 1990; anglers reported the first heavy emergence on 5 June. Spatial variation in timing was not adequately sampled with complete data from 2 sites only. Anglers rely on a steady upstream progression of the "hatch," and this is readily apparent in some years. In 1990 numerous adults were present on 28 May at the lower site, Valley of the Moon; a few were at Ranch Creek, and no exuviae were found at Bitterroot Flat. In 1989 anglers and I observed massive emergence all along the lower 80 km of Rock Creek on 5 June.

Densities, expressed as emergents per meter of shoreline (estimated densities per meter of stream length will be twice these values), appear high although few data exist for comparison. At Ranch Creek, *Pteronarcys* and *Calineuria* attained peak emergences of 5–7 m^{-1} d^{-1}. Cumulatives for Ranch Creek were *Pteronarcys* 19.6 m^{-1} yr^{-1}, *Calineuria* 40.0 m^{-1} yr^{-1}, and *Hesperoperla* 5.3 m^{-1} yr^{-1}. Incomplete data for 1989 (Fig. 3) yielded 13.9 *Pteronarcys* m^{-1} yr^{-1}, of similar magnitude to 1990. Catches at Bitterroot Flat were considerably less: *Pteronarcys* 6.0 m^{-1} yr^{-1}, *Calineuria*

7.6 m^{-1} yr^{-1}, and *Hesperoperla* 7.7 m^{-1} yr^{-1}. An interesting perspective is obtained by calculating that 1 adult of the combined species emerged in 1.5 cm of shoreline at Ranch Creek and in 4.7 cm at Bitterroot Flat.

Determination of sex ratios and sexual phenology of emergents is a necessary first step toward understanding operational sex ratios and mating tactics (Stewart 1994). Sex ratios (Table 1) were female-biased in *Pteronarcys* at both sites although not significantly so (χ^2 test); ratios at the 2 sites are not different ($P > 0.99$), nor do the combined data depart significantly from a 1:1 sex ratio ($P > 0.10$). Sex ratios of *Hesperoperla* were female-biased, significantly so for the larger collection, not different ($P > 0.99$) at the 2 sites, and significantly ($P < 0.005$) biased in the combined data. *Calineuria*, in contrast, was strongly male-biased at Ranch Creek, not different ($P > 0.10$) at the 2 sites, and significantly ($P < 0.005$) male-biased in combination. These results suggest very different mating systems, especially when comparing the 2 Perlidae.

TABLE 1. Sex composition by species and locations.

Species	Location	Male	Female
Pteronarcys	Ranch	93	121
	Bitterroot	25	34
Calineuria	Ranch	175	120
	Bitterroot	37	37
Hesperoperla	Ranch	16	29
	Bitterroot	24	49

Operational sex ratios also depend on sex-specific emergence phenology and on the functional life span, especially of males, which probably can mate more than once. Longevity was not measured in this study. Differential emergence by sex (Table 2) illustrates the protandrous pattern seen in many insects. Median males of *Pteronarcys* and *Calineuria* emerged 2–3 d before median females. Differences in distributions of emergence times of the sexes were tested with Kolmogorov-Smirnov tests (2-tailed). Contrasts involving *Pteronarcys* and *Calineuria* were significant except for *Pteronarcys* at Bitterroot Flat where sample size was small and where late emergents, mentioned above, included males. The pattern for *Hesperoperla* was quite different. Median emergence dates were very similar, especially in view of the extended emergence of this species (Fig. 2), and distributions of emergence times by sex were not significantly different.

Attributes other than sex may vary through the emergence period. A tendency for early emergents to be larger than later ones has been reported in stoneflies (Khoo 1964, Sheldon 1972) and other insects. Examination of size vs. time plots suggested that such patterns were weak or absent in these species. Formal tests and metrics were based on 2 × 2 tables divided at medians of size and time. A significant χ^2 indicates that size and emergence time are not independent and the phi-coefficient (a nonparametric correlation coefficient with range -1 to $+1$) measures the strength and direction of the interaction. Size-time interactions (Table 2) were weak and only 3 of 11 tests were significant. Seven of 11 phi-coefficients were negative; i.e., later individuals were smaller, including all the significant cases. Effects on females were stronger than males in all species and locations. The collective result indicates little or no size change through the relatively short emergence periods of these species. If fitness attributes such as fecundity and mating success are size-dependent, quality of potential mates varies little over time. This conclusion may depend in part on the conservative contingency test used. Blackburn et al. (1993) showed that, in sampling from skewed size distributions, size and abundance were confounded. To avoid this effect, I used a nonparametric test. Applying the same test to comparable data (Sheldon 1972) on male *Skwala curvata* (Hanson) (Perlodidae) yields phi $= -0.48$, $P < 0.005$, a much stronger size-time interaction than observed in Rock Creek stoneflies. Although conservative, the tests can detect temporal size patterns where they exist.

Natural history observations on post-emergents include the following. Adults are readily apparent on bushes where mating occurs. Oviposition flights, occurring as air temperatures rise, appear to be directed upstream, and many flying adults of *Pteronarcys* were observed several kilometers upstream from reaches where, from exuvial density and number of adults on bushes, significant emergence had occurred. Supporting Muttkowski's (1929) observations on predation, I saw numerous birds, especially flocks of 30–40 Western

TABLE 2. Emergence timing and size trends by sex (M, F) and location. Median dates are all in June 1990 and probabilities are from Kolmogorov-Smirnov contrasts of temporal distributions of emergence of the 2 sexes. Correlations (phi) are negative if later emergers are smaller; probabilities from χ^2.

		Median date			Size-time (M)		Size-time (F)	
Species	Site	M	F	*P*	phi	P	phi	*P*
Pteronarcys	Ranch	3	5	<0.001	–0.02	>0.75	+0.05	>0.50
	Bitterroot	4	6	>0.05	+0.04	>0.75	–0.26	>0.10
Calineuria	Ranch	17	20	<0.001	–0.17	<0.025	–0.30	<0.005
	Bitterroot	15	18	<0.001	–0.17	>0.75	+0.13	>0.25
Hesperoperla	Ranch	10	11	>0.40	—	—	–0.14	>0.25
	Bitterroot	13	13	>0.90	–0.11	>0.50	–0.32	<0.05

Tanagers (*Piranga ludoviciana*), foraging in riparian vegetation and hawking at flying adults, particularly *Pteronarcys*.

DISCUSSION

The simple emergence traps worked well at the 2 sites where stream banks were steep enough that a moderate rise in water level did not submerge the entire trap. Daily maintenance was necessary to accommodate fluctuating discharge and to yield temporally precise emergence data. Data aggregated over longer periods can be very useful (Masteller 1983, Kuusela 1984) but miss the details of short, synchronous emergences.

Although common elements appear, each of the 3 species had unique elements in its emergence phenology. *Pteronarcys* and *Calineuria*, although intraspecifically synchronous, were temporally well separated whereas the less abundant *Hesperoperla* had a longer, less synchronous emergence overlapping the other two. Synchrony has been suggested as a tactic for satiating predators (Sweeney and Vannote 1982); perhaps *Hesperoperla* benefits from emerging with abundant *Calineuria*.

Patterns of size and sex ratio also vary between species. A general tendency toward protandrous emergence in insects is supported in *Pteronarcys* and *Calineuria*, species with short, synchronous emergence periods. The selective advantage (Fagerström and Wiklund 1982) of protandry apparently is reduced in the less common *Hesperoperla* with its protracted emergence. Size-time interactions were weak although females showed a greater tendency than males for early emergents to be larger. The conservative nonparametric statistics used here may have failed to detect real phenomena. However, Blackburn et al. (1993) have shown that skewed size distributions and temporally varying collection sizes, as in most emergence data, can produce statistically "significant" artifacts with parametric tests.

Repeatability of observations is an important issue. Emergence biology of *Pteronarcys* in Rock Creek is very similar to the same species in Colorado (DeWalt and Stewart 1995). The differences in numbers and species proportions at Ranch Creek and Bitterroot Flat may indicate a longitudinal trend, but I attribute them to differences in pool:run:riffle proportions and other physical factors. Phenology and sex ratios were similar at the 2 sites. Haro et al. (1994) detected substantial variation of size and sex ratio of a perlodid stonefly among sites and years.

Emergence is a single event in a life history. Emphasis in this paper is on timing, identity, size, and sex of emergents. More generally, emergents are the product of the aquatic phase of the life history and input to the adult population. Emergence data could be a sensitive indicator of nymphal population biology and environmental conditions between years and locations (Haro et al. 1994). Of equal interest, the numbers and quality (sex, size) of emergents must influence mating behavior and reproductive success. Detailed studies of stonefly reproduction (Alexander and Stewart 1996) would be enhanced by a firm comparative base of emergence data. Such data are relatively easy to obtain and, for *Pteronarcys* and the perlids of Rock Creek, provide information at the time of high discharge when the stream itself is unworkable.

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COMPETITION AND NICHE PARTITIONING AMONG *PSEUDOROEGNERIA SPICATA, HEDYSARUM BOREALE,* AND *CENTAUREA MACULOSA*

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ABSTRACT.—Maximizing desired plant diversity has been suggested as a means of minimizing non-indigenous plant invasion on rangeland by maximizing niche occupation. Competition between 2 desired indigenous species, *Pseudoroegneria spicata* (Pursh.) Löve (bluebunch wheatgrass) and *Hedysarum boreale* Nutt. var. *boreale* (northern sweetvetch), and a non-indigenous invader, *Centaurea maculosa* Lam. (spotted knapweed), was quantified using growth of isolated individuals and 2 three-species addition series experiments. Seeding densities of *P. spicata* remained constant at 0, 200, 400, and 800 seeds m^{-2} in both experiments. *H. boreale* and *C. maculosa* seeding densities were 0, 200, 400, and 800 seeds m^{-2}, respectively, in the 1st experiment and 0, 400, 800, and 1600 seeds m^{-2}, respectively, in the 2nd experiment. Densities were factorially arranged. Pots were placed in an environmental chamber (12°C, 12-h day length, 200 µmol photons m^{-2} s^{-1} spectral light) in a randomized-complete-block design. After 90 d the growth rate of *P. spicata* (92.1 mg d^{-1} shoot growth) was greater than that of the 2 forbs (1.6 and 5.5 mg d^{-1} for *H. boreale* and *C. maculosa*, respectively), and growth rates of the 2 forbs were similar to one another. Curvilinear regression indicated that intraspecific competition was more important in determining shoot weight than interspecific competition. In addition, the 2 forbs competed more directly with each other than with *P. spicata*. Competition coefficient ratios (1.42 and 1.53 for *P. spicata* with *H. boreale* and *C. maculosa*, respectively, and 1.03 for *H. boreale* with *C. maculosa*) indicated substantial partitioning of resources between *P. spicata* and each of the forbs. Little or no resource partitioning occurred between forbs. This study suggests that increasing desired plant diversity may minimize weed invasion by increasing niche occupation.

Key words: plant diversity, three-species addition series, competitive relationships, resource preemption, niche partitioning, spotted knapweed, Centaurea maculosa, Pseudoroegneria spicata, Hedysarum boreale.

The ecological integrity and environmental quality of grassland and sagebrush/grassland ecosystems of western North America are being degraded by non-indigenous invasive plants. These ecosystems, once dominated by species such as *Artemisia tridentata* Nutt. (big sagebrush), *Pseudoroegneria spicata* (bluebunch wheatgrass), *Festuca scabrella* Torr. (rough fescue), and *Festuca idahoensis* Elmer (Idaho fescue), now contain extensive areas dominated by non-indigenous weeds such as *Centaurea solstitialis* L. (yellow starthistle; Maddox 1983), *Bromus tectorum* L. (cheatgrass; Mack 1981), *Euphorbia esula* L. (leafy spurge; Lajeunesse et al. 1997), and *Centaurea maculosa* Lam. (spotted knapweed; Sheley et al. 1998). It is widely accepted that invasion of rangeland by these species reduces resource values, including species diversity, forage production, wildlife habitat, and ecosystem function (Lacey et al. 1989, Olson and Lacey 1990, Thompson 1996).

It has been hypothesized that long-term, sustainable management of ecosystems under invasion by exotic species must focus on promoting or establishing desirable species with plant traits that maximize niche occupation (Larson et al. 1994, Sheley et al. 1996). Many aggressive exotic invaders appear to be able to occupy most niches in plant communities they invade. For example, Sheley and Larson (1996) suggested that *Centaurea diffusa* Lam. (diffuse knapweed) monotypically dominates rangeland by maximizing niche occupation through developing a hierarchy of age classes within the population. In native communities establishment of desirable species having diverse above- and belowground growth forms may minimize interspecific competition, maximize vertical and temporal structure, and enhance their resource capture (Pyke and Archer 1991, Tilman 1996). Maximizing vertical and temporal resource capture by increasing the diversity of desirable species may limit exotic invasion

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through resource preemption (Sheley and Larson 1995).

Our objective was to develop an initial understanding of the effect of combining desirable plant species with contrasting above- and belowground growth forms on their interactions with *C. maculosa*. Because *C. maculosa* is a taprooted forb, we hypothesized that the addition of a desirable taprooted forb in a grass population would increase interspecific competition by maximizing niche occupation and reduce *C. maculosa* growth. We compared growth rates and competitive interactions among *P. spicata*, *Hedysarum boreale* Nutt. var *boreale* (northern sweetvetch), and *C. maculosa* using growth analysis and addition series methods.

MATERIALS AND METHODS

We used 2 indigenous species, *H. boreale* and *P. spicata*, as desired species. *C. maculosa*, a non-indigenous perennial invasive weed, currently dominates about 2.4 million ha of rangeland and open forest throughout western North America (Sheley et al. 1998). Habitat types dominated by *P. spicata* are commonly invaded by *C. maculosa*. *H. boreale*, a deep-taprooted legume found throughout the Northwest (Hitchcock et al. 1977), occurs on sagebrush slopes and plains and in open grasslands (Isley 1955). We chose *H. boreale* because its taproot appears to allow this species to occupy a more similar belowground niche to that of *C. maculosa* than to a fibrous-rooted grass. Therefore, *H. boreale* should compete more directly with *C. maculosa* than with *P. spicata*.

Seeds of *C. maculosa* were collected from Gallatin County, Montana, in August 1995. *P. spicata* (Goldar variety) and *H. boreale* seeds were purchased from Granite Seed Co., Lehi, Utah, in September 1995.

Individual Growth of Isolated Plants

Isolated individuals of each species were gown in poly-vinyl-chloride (PVC) pots to compare intrinsic growth rates of the species. Pots were 15 cm in diameter and 100 cm deep and were filled with a pasteurized, sifted (10-mm sieve) soil mixture of 2/3 Farland silt loam (fine-silty, mixed Typic Argiboroll) and 1/3 sand. Soil was saturated with water and allowed to equilibrate to pot capacity. Ten seeds were broadcast on the soil surface and covered with less than 2 mm of dry soil. The soil surface was kept moist for the 1st wk of the study by fog misting and then covering with clear plastic. No additional watering took place.

One week after emergence, plants were thinned to 1 plant per pot. Each species had 6 harvest dates at 14-d intervals beginning 14 d after thinning. There were 4 replications at each harvest date. Pots were arranged in an environmental chamber (12°C, 12-h day length, 200 μmol photons m^{-2} s^{-1} spectral light) in a randomized-complete-block design.

Harvesting involved manually washing soil from the roots. Roots were cut from shoots, root length was scanned using a Comair root-length scanner (Comair Corp., Melbourne, Australia), and leaf area was measured using a Licor-3100 area meter with conveyer belt (LI-COR, Inc., Lincoln, NE). Roots and shoots were then dried to a constant weight at 60°C for 48 h and weighed. Root length, root weight, leaf area, shoot weight, and total weight of isolated individuals were incorporated into linear regression equations as dependent variables with time as the independent variable.

Differences of growth rates between 2 species were calculated using the variance ratio determined by the extra sums of squares procedure for comparing slopes (Ratkowsky 1983, Milliken and Milliken-MacKinnon 1998). The equation used was

$$F = \{(RSS_c - RSS_s)/(df_c - df_s)\}/(RSS_s/df_s).$$

RSS_c and df_c are residual sums of squares and degrees of freedom, respectively, for regressions run using pooled data of 2 species. RSS_s and df_s are residual sums of squares and degrees of freedom, respectively, for regressions run using the separate data for the 2 species. A variance ratio larger than the critical $F(\alpha = 0.05, df_{numerator}, df_{denominator})$ value rejects the null hypothesis that the slopes are the same.

Competition Experiments

Monocultures and mixtures of *P. spicata*, *H. boreale*, and *C. maculosa* were arranged to provide 2 addition series experiments with total stand densities ranging from 25 to 1650 plants m^{-2} (Spitters 1983, Radosevich 1987). The *P. spicata*:*H. boreale*:*C. maculosa* seeding densities in experiment 1 were factorially arranged combinations of 0, 100, 400, and 800 seeds m^{-2}. Seed production of *C. maculosa* on infested rangeland in Montana (Jacobs and Sheley 1998), Washington and Idaho (Shirman 1981) falls within this range. Recommended seed rate for *P. spicata* ranges from 277 to 484 seeds m^{-2} (Holzworth and Lacey 1991) and for *H. boreale* is 125 seeds m^{-2} (Granite Seed Co. 1996). In experiment 2 seeding densities of *H. boreale* and *C. maculosa* were doubled (0, 200, 800, 1600 seeds m^{-2}) because of low establishment of these species in experiment 1. Seeding densities of *P. spicata* were the same as experiment 1, as were potting conditions.

Pots, soil, establishment conditions, and growth chamber conditions for the competition experiments were the same as described for the growth of isolated individuals with the exception that seeds were broadcast on the soil surface and manually arranged until a uniform distribution was achieved. There was no hand thinning of established plants.

Ninety days after emergence plants in each pot were clipped at the soil surface, separated by species, dried to constant weight at 60°C for 48 h, and weighed. Shoot weights for the 3 species were used to determine competitive interactions using nonlinear procedures (Proc Nlin; SAS Institute 1991). Regression equations were of the following forms (Watkinson 1984):

P. spicata W_w =

$$Wm_w[1 + A_w(N_w + C_{wv}N_v + D_{wk}N_k)]^{-Bw}$$

H. boreale W_v =

$$Wm_v[1 + A_v(N_v + C_{vw}N_w + D_{vk}N_k)]^{-Bv}$$

C. maculosa W_k =

$$Wm_k[1 + A_k(N_k + C_{kw}N_w + D_{kv}N_v)]^{-Bk}.$$

W_w, W_v, and W_k are the mean shoot weights per plant of *P. spicata*, *H. boreale*, and *C. maculosa*, respectively. Wm_w, Wm_v, and Wm_k are the mean weights per plant grown in isolation and were derived for each species from the individual growth of isolated plants. A_w, A_v, and A_k represent the area required by a plant to achieve Wm, and in this experiment they indicate area of the pot. N_w, N_v, and N_k are the densities of *P. spicata*, *H. boreale*, and *C. maculosa*, respectively. C_{wv}, D_{wk}, C_{vw}, D_{vk}, C_{kw}, and D_{kv} are the per plant equivalents of w, v, and k and can be interpreted as the ratio of intra:interspecific competition between the subscripted species. Negative B_w, $-B_v$, and $-B_k$ are the efficiencies of resource utilization by the populations and were estimated to be 1 (Firbank and Watkinson 1985). The model uses the data to estimate C_{wv}, D_{wk}, C_{vw}, D_{vk}, C_{kw}, and D_{kv} and provides a 95% confidence interval around its mean. If C_{wv}, D_{wk}, C_{vw}, D_{vk}, C_{kw}, and $D_{kv} > 1$, intraspecific competition had a greater effect on plant weight. If C_{wv}, D_{wk}, C_{vw}, D_{vk}, C_{kw}, and $D_{kv} < 1$, interspecific competition had a greater effect on plant weight.

Partitioning of resources between *P. spicata* and *H. boreale*, *P. spicata* and *C. maculosa*, and *H. boreale* and *C. maculosa* was calculated using the competition coefficients from nonlinear regressions in the equation $(1/C_{xz})(C_{zx})$ (Spitters 1983, Connolly 1986, Joliffe 1988). Deviations from unity indicate increased resource partitioning (niche separation).

RESULTS AND DISCUSSION

Individual Growth of Isolated Plants

Growth rates measured from root and shoot weight, root length, and leaf area were greater for *P. spicata* than *C. maculosa* and *H. boreale* (Tables 1, 2). Root growth measured by weight was greater for *P. spicata* (69.5 mg d^{-1}) compared to *H. boreale* (2.1 mg d^{-1}) and *C. maculosa* (6.4 mg d^{-1}). Based on shoot weight, *P. spicata* growth rate was 92.1 mg d^{-1} compared to 1.6 mg d^{-1} for *H. boreale* and 5.5 mg d^{-1} for *C. maculosa*. Root length and leaf area growth rate was 8 times greater for *P. spicata* than *H. boreale* and *C. maculosa*. *H. boreale* root length and leaf area growth was greater than that of *C. maculosa*. There was no difference between *H. boreale* and *C. maculosa* in root weight; however, *C. maculosa* shoot weight increased faster than that of *H. boreale*.

P. spicata rate of soil depth penetration (10.1 cm d^{-1}) was greater than that of *C. maculosa* (7.1 cm d^{-1}), but not that of *H. boreale* (8.0 cm d^{-1}; Tables 1, 2). Rates of soil depth penetration were not different between *C. maculosa* and *H. boreale*.

Soil moisture is depleted first from the upper soil horizon in semiarid ecosystems (Daubenmire 1970). Reichenberger and Pyke (1990) found that survival of *P. spicata* seedlings increased with greater depth of root competition with big sagebrush. Rapid growth

TABLE 1. Growth rates per day (harvest date is the independent variable) for root length, leaf area, root weight, shoot weight, and soil penetration (dependent variables) of isolated individual *Pseudoroegneria spicata* (PSSP), *Centaurea maculosa* (CEMA), and *Hedysarum boreale* (HEBO) determined from linear regression equations.

Species	Root length (mm d^{-1})	R^2	Leaf area (cm^2)	R^2	Root weight (mg d^{-1})	R^2	Shoot weight (mg d^{-1})	R^2	Soil penetration (cm d^{-1})	R^2
PSSP	564	0.53	13.6	0.62	69.5	0.58	92.1	0.58	10.1	0.90
HEBO	73	0.48	4.1	0.19	2.1	0.72	1.6	0.74	8.0	0.76
CEMA	69	0.78	1.0	0.42	6.4	0.65	5.5	0.14	7.1	0.42

TABLE 2. Variance ratios using the extra sums of squares procedure comparing slopes (growth rate d^{-1}) of the regressions between 2 species in Table 1. Critical $F_{(.05,42,43)} = 1.65$ for rejecting the null hypothesis that the slopes are the same.

Species compared	Root length	Leaf area	Root weight	Shoot weight	Soil penetration
PSSP:CEMA[a]	19.2	8.8	24.8	30.0	5.55
PSSP:HEBO	16.4	8.9	9.1	16.1	1.03
CEMA:HEBO	17.6	3.2	1.2	7.0	0.53

[a]Species names listed in Table 1.

TABLE 3. Competition coefficients, upper and lower confidence intervals ($P = 0.05$), and coefficient of determination values (R^2) from curvilinear regression equations using species harvest densities to predict shoot weight of *Pseudoroegneria spicata* (PSSP), *Hedysarum boreale* (HEBO), and *Centaurea maculosa* (CEMA).

Dependent species	Competition species	Competition coefficient	Lower confidence interval	Upper confidence interval	R^2
PSSP	HEBO (C_{wv})	5.0	1.5	8.6	0.52
	CEMA (D_{wk})	3.9	0.4	7.4	
HEBO	PSSP (C_{vw})	7.1	4.2	9.9	0.39
	CEMA (D_{vk})	3.0	0.6	5.3	
CEMA	PSSP (C_{kw})	6.0	6.6	8.4	0.33
	HEBO (D_{kv})	2.9	1.0	4.9	

rate is believed to give a plant an advantage over its neighbors because it is able to preempt their resource use (Harper 1980). Under the conditions of our study, and when emergence times and duration of growth are equal, the rapid growth rate and soil depth penetration of *P. spicata* give it an advantage over *C. maculosa* and *H. boreale* of capturing both above- and belowground resources. Root length and leaf area results suggest that *H. boreale* may have a slight advantage over *C. maculosa*.

The rapid relative growth rate of *B. tectorum* has been used to explain its dominance on *P. spicata* range (Harris 1967). Sheley and Larson (1994) found the growth of *C. solstitialis*, another member of the knapweed group of plants, was 7 times greater than that of *B. tectorum*. The success of *C. maculosa* over *P. spicata* under field conditions may be due, in part, to its longer duration of growth (Jacobs and Sheley 1998) rather than its intrinsic growth rate.

Competition Series

Intraspecific interference was more important than interspecific interference for the prediction of shoot weight for the 3 species (Table 3). The influence of *P. spicata* density on its own shoot weight was 5 times greater than *H. boreale* density, and 4 times greater than *C. maculosa* density (Table 3, Fig. 1). However, the confidence interval for *C. maculosa* density predicting *P. spicata* weight includes 1, suggesting that *C. maculosa* density is as important in predicting *P. spicata* weight as *P. spicata* density. These results suggest that

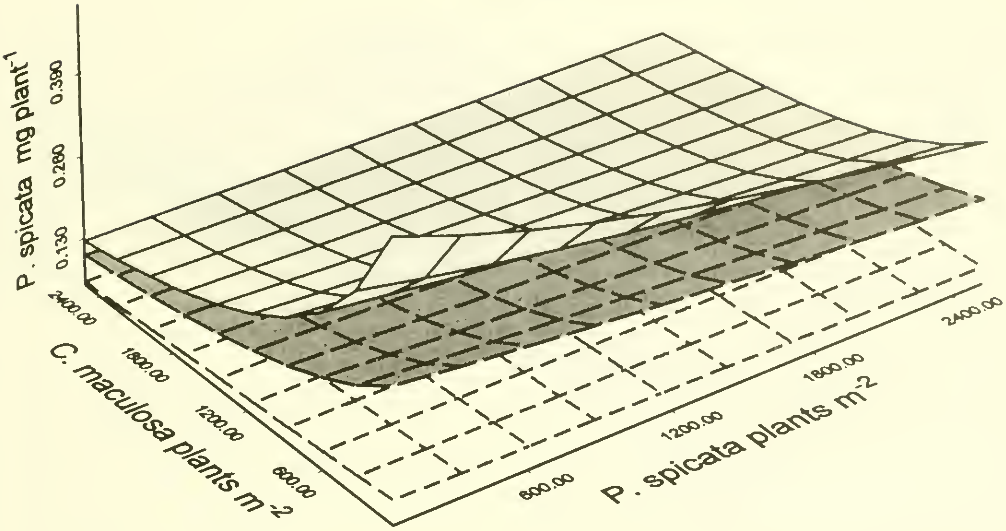

Fig. 1. Response surfaces using *P. spicata*, *H. boreale*, and *C. maculosa* density (plants m^{-2}) to predict *P. spicata* shoot weight (mg $plant^{-1}$) with the equation $W_w = 0.54\{1 + 0.0182(N_w + 3.9N_k + 5N_v)\}^{-1}$. The light shaded surface has an *H. boreale* density (N_v) of 0, the dark shaded surface $N_v = 500$ plants m^{-2}, and the unshaded surface $N_v = 1500$ plants m^{-2}.

including *H. boreale* with *P. spicata* in a plant community will have less impact on *P. spicata* than on *C. maculosa.*

Competition coefficients using plant density to predict *H. boreale* shoot weight show *H. boreale* density was 7 times more important than *P. spicata* density and 3 times more important than *C. maculosa* (Table 3, Fig. 2). The confidence interval for the coefficient predicting the importance of *C. maculosa* density on *H. boreale* shoot weight includes 1, suggesting that *C. maculosa* is as important as *H. boreale* density for predicting *H. boreale* weight. We conclude that *H. boreale* competes more directly with *C. maculosa* than with *P. spicata.*

Regressions predicting *C. maculosa* shoot weight showed *C. maculosa* density 6 times more important than *P. spicata* density and 3 times more important than *H. boreale* density (Table 3, Fig. 3). Only the confidence interval for the coefficient predicting *H. boreale* density effect on *C. maculosa* shoot weight included 1, suggesting that *H. boreale* density may have the same impact on *C. maculosa* shoot weight as *C. maculosa* density. These results show that the 2 forbs have a greater impact on each other's shoot weights than on *P. spicata* shoot weight and suggest that there is some niche overlap between the 2 species.

Niche partitioning between these forbs and the grass was evident from competition coefficient ratios. The coefficient ratio of *C. maculosa:H. boreale* was 1.03, close to unity, showing little or no niche partitioning. Ratios testing *P. spicata* with *C. maculosa* or *H. boreale* were 1.42 or 1.53, respectively, indicating greater niche partitioning between grass and forbs than between the forbs.

Competition in semiarid plant communities is an important determinant of community structure (Fowler 1986). Our results support the theory that combining desirable plant species with contrasting above- and belowground growth forms will maximize niche occupation and may increase resource preemption (Pyke and Archer 1991, Sheley et al. 1996, Tilman 1996). Growth characteristics of *H. boreale* were more similar to those of *C. maculosa* than *P. spicata*, and *H. boreale* competed more directly with *C. maculosa* than with *P. spicata.* We expect *H. boreale* to coexist with *P. spicata* because our results suggest that these 2 species effectively partition resources and minimize competitive exclusion.

The hypothesis that greater species diversity reduces community invasibility by increasing niche occupation and facilitating more complete use of limiting resources is being proposed as a sustainable weed management

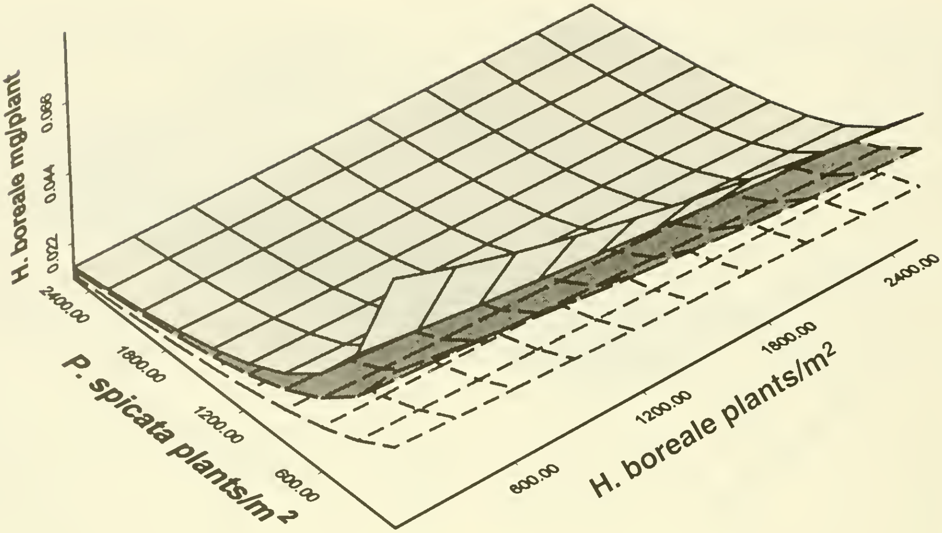

Fig. 2. Response surfaces using *P. spicata*, *H. boreale*, and *C. maculosa* density (plants m^{-2}) to predict *H. boreale* shoot weight (mg $plant^{-1}$) with the equation $W_v = 0.05\{1 + 0.0182(N_v + 7.1N_w + 3N_k)\}^{-1}$. The light shaded surface has a *C. maculosa* density (N_k) of 0, the dark shaded surface $N_k = 500$ plants m^{-2}, and the unshaded surface $N_k = 1500$ plants m^{-2}.

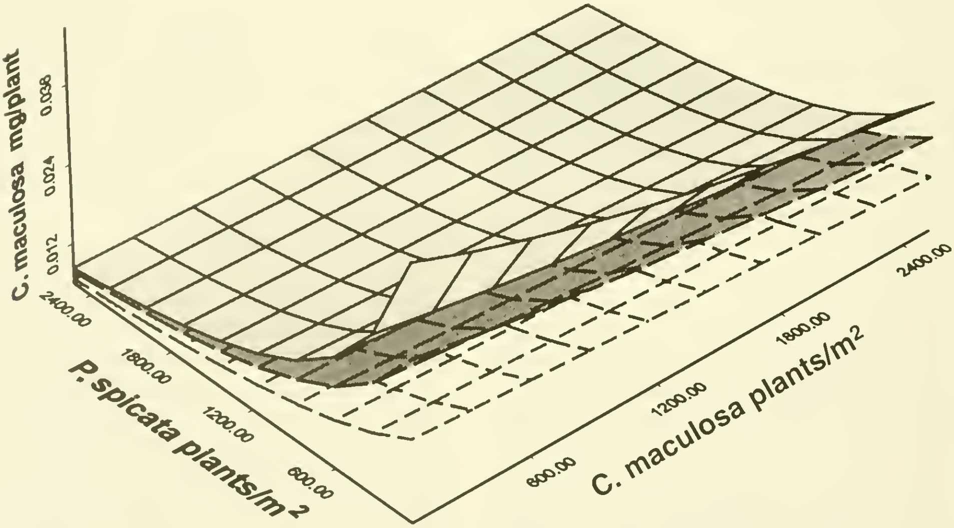

Fig. 3. Response surfaces using *P. spicata*, *H. boreale*, and *C. maculosa* density (plants m^{-2}) to predict *C. maculosa* shoot weight (mg $plant^{-1}$) with the equation $W_k = 0.1\{1 + 0.0182(N_k + 3.9N_w + 5N_v)\}^{-1}$. The light shaded surface has an *H. boreale* density (N_v) of 0, the dark shaded surface $N_v = 500$ plants m^{-2}, and the unshaded surface $N_v = 1500$ plants m^{-2}.

strategy on rangeland (McNaughton 1993, Robinson et al. 1995, Sheley and Larson 1995, Tilman 1997). Our study supports this hypothesis and suggests that maintaining taprooted forbs along with caespitose grasses increases niche occupation and may be more effective in minimizing invasion of taprooted weeds than the grasses alone. Together they maximize resource capture and preempt resource use by weeds (Sheley et al. 1996).

Acknowledgments

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A NEW SPECIES OF *PLECIA* FROM THE GREEN RIVER FORMATION AND NEW COMBINATIONS OF FOSSIL BIBIONIDAE (DIPTERA)

Scott J. Fitzgerald[1]

ABSTRACT.—*Plecia akerionana*, n. sp., is described from the Green River Formation, Colorado, and diagnosed with *P. minutula* Rice, *P. myersi* Peterson, and *P. rhodopterina* Cockerell. *Plecia intermedia* (Scudder), the genotype of *Mycetophaetus*, and *Plecia creedensis* James are transferred to the genus *Penthetria*, and *Hesperinus immutabilis* Melander is transferred to *Plecia*.

Key words: Diptera, Bibionidae, fossil, Plecia, *new species, Green River Formation.*

Over 20 fossil species in 5 genera of Bibionidae have been described from the shales of Florissant, Colorado (Oligocene), while only 4 species, all belonging to the genus *Plecia*, have been described from the Green River Formation, Colorado/Wyoming/Utah (Eocene). Although there are few bibionid species known from the Green River Formation, they are among the more abundant Diptera, as was found in a survey of several sites in the Parachute Creek Member of the Green River Formation (Codington 1993) in which Bibionidae represented 22% of Diptera specimens. One Green River site (site F-1, Wyoming) is particularly rich in bibionid specimens, with 80–96% of all insects representing *Plecia pealei* Scudder (Scudder 1890, Grande 1984).

This study describes an additional species of *Plecia* from the Green River Formation, Colorado, and reassesses generic assignments of several other fossil bibionids described from Colorado.

Morphology follows McAlpine (1981). Measurements were made with an ocular micrometer. Wings were illustrated with the aid of a camera lucida. The following individuals made materials available for study: Philip Perkins and Michael Kelley, Museum of Comparative Zoology, Harvard University (MCZC); Virginia Scott (entomology) and Peter Robinson (paleontology), University of Colorado, Boulder (UCMC); Conrad Labandeira and Mark Florence, National Museum of Natural History, Smithsonian Institution (USNM). Specimens have been deposited at these institutions.

Genus *Plecia* Wiedemann

Plecia Wiedemann, 1828: 72. Type species: *Hirtea fulvicollis* Fabricius, 1805, by subsequent designation of Blanchard (1840: 576).

Plecia akerionana Fitzgerald, **new species**

(Figs. 1–3)

HOLOTYPE.—♀, USA: COLORADO: Rio Blanco County, 4 mi W Rio Blanco, Bob Hammon (USNM #498201).

ETYMOLOGY.—The specific epithet is derived from the Greek *akerios* (lifeless) and *nan* (dwarf).

DISCUSSION.—*Plecia akerionana* was collected from the upper Parachute Creek member of the Green River Formation (Lake Uinta Locality U-2 [of Grande 1984]) and is estimated to be 45–47 million yr old (Dayvault et al. 1995).

DIAGNOSIS.—*Plecia akerionana* can be distinguished from most other North American fossil *Plecia* by its minute size and is most similar in size to *P. rhodopterina* Cockerell (Green River Formation, Colorado, Eocene), *P. myersi* Peterson (Canadian amber, Cretaceous), and *P. minutula* Rice (British Columbia, Eocene). Table 1 provides wing measurements for comparison of the 4 smallest (based on wing length) species of Nearctic *Plecia*. *Plecia akerionana* is most similar to *P. myersi* but can be distinguished by the longer and relatively narrower

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TABLE 1. Comparison of wing measurements of the 4 smallest Nearctic fossil *Plecia* species (*P. minutula* Rice, *P. rhodopterina* Cockerell, *P. akerionana*, n. sp., and *P. myersi* Peterson) using methods of Rice (1959) and Melander (1949); measurements of *P. minutula* and *P. myersi* are taken from Rice (1959) and Peterson (1975), respectively. Wing measurements in mm.

	minutula	*rhodopterina*	*akerionana*	*myersi*
Rice (1959)[a]				
WL	5.3	5.00	3.47	2.70
WW	2.2	2.16	1.32	1.20
RL	3.1	3.12	2.45	1.92
AxC	0.63	0.62	0.36	0.35
R3+4	1.0	0.84	0.38	0.35
R5	1.8	1.64	0.99	0.50
SC	0.38	0.34	0.19	0.20
RF	1.4	1.54	1.40	1.07
RAx	0.9	0.86	0.57	0.47
MC	0.35	0.20	0.15	0.07
Melander (1949)[b]				
A-B	*	0.86	0.57	0.47
A-C	*	1.92	1.32	1.10
A-E	*	1.54	1.40	1.07
A-L	*	3.20	2.39	1.87
B-G	*	0.38	0.17	0.22
B-J	*	0.22	0.15	0.07
C-D	*	0.40	0.34	0.20
C-F	*	1.36	1.20	0.90
C-P	*	0.22	0.23	0.17
D-F	*	1.04	0.82	0.65
D-H	*	0.34	0.19	0.20
E-D	*	0.84	0.38	0.30
E-F	*	1.64	0.99	0.82
M-J	*	0.44	0.67	0.50
M-K	*	0.76	0.88	0.75
N-O	*	0.70	0.57	0.52
P-R	*	0.18	0.23	0.20

[a] Key to wing measurements of Rice (1959): WL = wing length; WW = wing width (at point of Rm crossvein; Rice does not indicate at what point this measurement is taken); RL = length of radial sector; AxC = distance between Rm crossvein and costa; R_{3+4} = length of R_{2+3} from fork to tip; R_5 = length of R_{4+5} from fork to tip; SC = height of submarginal cell at tip of R_{2+3}; RF = distance between origin of radial sector and its fork; RAx = distance between origin of radial sector and Rm crossvein; MC = height of cell sc (marginal cell) at point of Rm crossvein.

[b] For key to wing measurements see Melander (1949) or Peterson (1975).

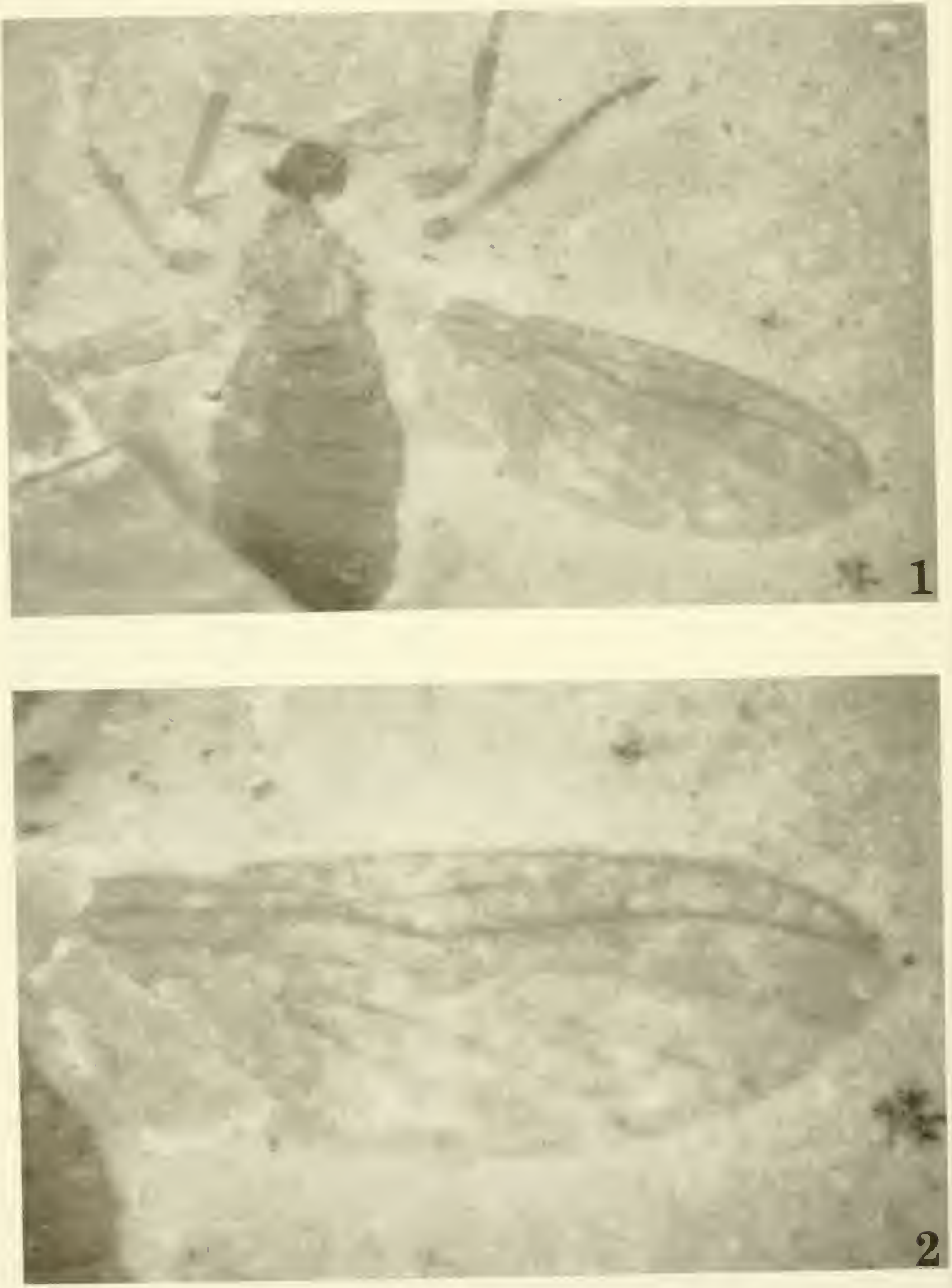
*Measurement not available.

wing (Table 1), younger age, and ratio of the Rm crossvein to the pedicel of M_{1+2} 1:1.5 in *P. akerionana* and 1:3 in *P. myersi*. However, due to the difference in age, locality, and type of preservation, *P. akerionana* more likely would be confused with *P. rhodopterina*, which can be distinguished by the longer, relatively wider wing (Table 1, Fig. 4) and R_{2+3} straight (Fig. 4) rather than evenly curved (Figs. 2, 3).

The 4 *Plecia* species known from the Green River Formation are, based on wing length, significantly larger and thus easily distinguished from *P. akerionana*: *P. dejecta* Scudder (wing 7.5 mm long × 3.0 mm wide), *P. pealei* (10.0 mm × 3.5 mm), *P. rhodopterina* (5.00 mm × 2.16 mm), and *P. woodruffi* Cockerell (7.0 mm × 2.75 mm).

GENERAL DESCRIPTION.—Compression fossil on pentagonal piece of light gray shale approximately 5 cm × 5 cm and 2.0–5.5 mm thick. Dorsoventrally preserved with wings and legs outstretched (Fig. 1). Reverse not present.

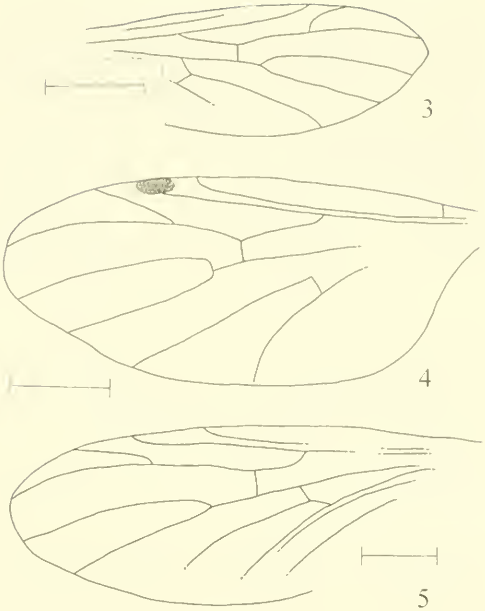
FEMALE.—Head dark brown. Left antenna with at least (basal segments difficult to distinguish) 9 round, compact segments, apical flagellomere small, nipple-like. Anteromedial region of head with 2 faint, segmented?, light brown structures (likely the labial palpi). Thorax and scutellum light brown. Legs (apex of right mid-femur, tibia, and 5 tarsomeres, apex of right fore femur, tibia, and 4? tarsomeres, apex of left mid-femur and tibia, and apex of left fore femur and tibia) brown with dense, short, dark brown, appressed hair. Apices of



Figs. 1–2. *Plecia akerionana*, photograph of holotype: 1, habitus; 2, wing.

fore tibiae more robust than that of mid-tibiae. Right fore and mid-tibiae with short, slender anteroapical spur. Right mid-basitarsus 0.40 mm long, 5 times as long as wide, tarsomere two 0.17 mm long, tarsomeres three through five 0.50 mm long. Right fore basitarsus 0.54 mm long, 6.75 times as long as wide. Wings (anterobasal portion of left wing and right wing minus most of anal lobe) light brown fumose. Wing tip slightly pointed, without anteroapical emargination. Anterior veins (especially costa, subcosta, radius, radial sector, R_{2+3}, and R_{4+5}) dark brown, posterior veins lighter. Pterostigma absent. Pedicel of M_{1+2} 1.5 times as long as Rm crossvein. R_{4+5} 2.6 times as long as R_{2+3}. R_{2+3} relatively short and vertical, evenly rounded (Figs. 2, 3). See Table 1 for wing measurements. Abdomen dark brown, posterior end (tergites 8 on) concealed under rock layer. Posterior edge of each tergite with a thin darker brown line marking the division between tergites. Abdomen robust, somewhat swollen in appearance.

MALE.—Unknown.



Figs. 3–5. Interpretation of wing of holotype: 3. *Plecia akerionana*; 4. *Plecia rhodopterina*; 5. *Plecia immutabilis*. Bar = 1 mm.

Plecia immutabilis (Melander)
(Fig. 5)

Hesperinus immutabilis Melander, 1949: 20. Holotype (#112554) (USNM), USA: COLORADO: Florissant, Lacoe collection.
Plecia immutabilis (Melander), **new combination.**

DISCUSSION.—The family Hesperinidae (or subfamily Hesperininae of the Bibionidae depending upon current views of classification; treated here as Hesperinidae) is differentiated in part from the Bibionidae by the antennal flagellomeres slender, elongate, and antenna longer than the thorax (Hardy 1981, Rohdendorf 1991). This differs greatly from the antenna of typical Bibionidae, which have relatively short, stout antenna with compact flagellomeres. Examination of the holotype of *H. immutabilis* is not particularly helpful as the antennae are not visible, although based on wing venation (R_{2+3} oblique in relation to R_{4+5}) the specimen clearly belongs to *Hesperinus* or *Plecia* (Fig. 4). However, the photograph of paratype #112588 (USNM) of *H. immutabilis* provided by Melander (1949) reveals that the antenna are of the bibionid and not the hesperinid type. Melander (1949) also treats species of *Plecia* described by Cockerell as *Hesperinus* and apparently was not clear on the characters that distinguish these 2 genera. The shape of the antenna and the shorter R_{2+3}, oblique in relation to R_{4+5}, indicate this species belongs to the genus *Plecia*.

Genus *Penthetria* Meigen

Penthetria Meigen, 1803: 264. Type species: *Penthetria funebris* Meigen, 1804, by subsequent monotypy in Meigen (1804: 104).
Mycetophaetus Scudder, 1892: 20. Type species: *Mycetophaetus intermedius* Scudder, 1892, by monotypy, **new synonym.**

Penthetria creedensis (James)

Plecia creedensis James, 1938: 114. Holotype female (#4523) (MCZC), USA: COLORADO: slopes of Willow Creek near Creede.
Penthetria creedensis (James), **new combination.**

DISCUSSION.—Based on wing venation in the illustration of *P. creedensis* provided by James (1938: 115, Fig. 2) and examination of paratype #19117 (UCMC), this species belongs to the genus *Penthetria*. *Penthetria* can be differentiated from *Plecia* by R_{2+3} longer than and nearly parallel to R_{4+5}.

There seems to have been some confusion among early workers in distinguishing *Plecia* from *Penthetria* as Cockerell (1911), discussing the genus *Plecia* from Florissant, Colorado, states that "the genus is still found in the same region," referring to *Penthetria heteroptera* Say (extant Nearctic *Plecia* are found only in semitropical parts of the southeastern United States). Furthermore, historic specimens examined (UCMC), identified by James as "*Plecia heteroptera*," also represent *Penthetria heteroptera.*

Penthetria intermedia (Scudder)

Mycetophaetus intermedius Scudder 1892: 20. Syntypes (#3494, 3463; reverse of one another) (MCZC), USA: COLORADO: Florissant.
Plecia intermedia (Scudder) (as treated by Evenhuis 1994).
Penthetria intermedia (Scudder), **new combination.**

DISCUSSION.—Scudder (1892) erected the monotypic mycetophilid genus *Mycetophaetus* to include the species *intermedius.* Although finding formal synonymy of the genus has been nebulous, various authors have treated *Mycetophaetus* as an extinct genus of Hesperinidae (Rohdendorf 1974), Mycetophilidae (Carpenter 1992), and a junior synonym of *Plecia*, Bibionidae (Evenhuis 1994). Examination of the syntypes of *P. intermedius* and the illustration provided by Scudder (1892: Plate II, Fig. 5) clearly places this species in the bibionid genus *Penthetria*, which is differentiated from *Plecia* by R_{2+3} longer than and nearly parallel to R_{4+5} and from Hesperinidae by the short, compact antennal flagellomeres.

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ASSORTATIVE MATING IN SOLDIER BEETLES (CANTHARIDAE: *CHAULIOGNATHUS*): TEST OF THE MATE-CHOICE HYPOTHESIS

Ruth Bernstein[1] and Stephen Bernstein[1]

ABSTRACT.—Soldier beetles of 2 species, *Chauliognathus basalis* and *C. deceptus*, were examined to test the Crespi hypothesis that positive assortative mating by size is caused by mate choice. Specifically, we tested the prediction that if mate choice involves choosing the largest mate available, then mating individuals will be larger than nonmating individuals. Four samples were taken, at different times during the mating season, from each of 2 sites. Each sample consisted of mating pairs, nonmating males, and nonmating females. Some of the samples contained beetles of both species; others contained beetles of a single species. For each gender elytron lengths of mating individuals were compared with elytron lengths of nonmating individuals. We found no effect of mating status (mating vs. nonmating) on elytron lengths in samples that exhibited assortative mating (which occurs where 2 species coexist). Surprisingly, we found a consistent effect of mating status on elytron lengths in samples that did not exhibit assortative mating (which occurs where only 1 species exists). Our results do not support the mate-choice hypothesis. Instead, mate choice and assortative mating appear to be alternative mating patterns in which mate choice occurs where a single species exists and assortative mating occurs where 2 species coexist.

Key words: mate choice, assortative mating, soldier beetles, Chauliognathus deceptus, Chauliognathus basalis.

Positive assortative mating by size occurs when the body sizes of mating pairs are more similar than if they mated at random. This mating pattern has been observed in soldier beetles (*Chauliognathus*), as reported by Mason (1972), McCauley and Wade (1978), McLain (1982, 1984, 1985), and Bernstein and Bernstein (1998). The ultimate cause of positive assortative mating by size may be sexual selection, in which differences in reproductive success, caused by competition over mates, are related to body size (Andersson 1994). Alternatively, positive assortative mating by size may be an artifact of environmental factors, such as temporal or spatial covariance of body size among mating males and females.

Many hypotheses have been offered to explain assortative mating in arthropods (Crespi 1989). One of these is the mate-choice hypothesis, based on sexual selection, in which individuals choose larger mates because they benefit reproductively and are differently capable of exercising choice (Darwin 1871, Ridley 1983). Male choice involves a large-male mating advantage in male-male competition for females combined with a preference for larger females; female choice involves factors that increase large-female pairing probability combined with a preference for larger males (Crespi 1989). When male choice occurs in soldier beetles, it is most likely because larger females carry more eggs (Ridley 1983). When female choice occurs, the apparent preference may be due to the superior ability of larger males in overcoming the higher "resistance to mating" of larger females (McCauley and Wade 1978, McCauley 1981). A prediction of the mate-choice hypothesis is that the mean size of mating individuals will be larger than the mean size of nonmating individuals (Arnqvist et al. 1996). Most data on arthropods do, in fact, show this mating pattern, either for females or for both sexes (Crespi 1989).

In the study described herein, we examined the mate-choice hypothesis in 2 species of soldier beetles (*Chauliognathus deceptus* Le Conte and *C. basalis* Fender). These beetles mate conspicuously, occur in large populations, and remain coupled for many hours. (In a preliminary study with marked pairs, we found that 68% of mated pairs remained together for more than 5 h and 34% for more than 17 h). In a previous study (Bernstein and Bernstein 1998) we found positive assortative mating by body size in some populations but not in others. Arnqvist et al. (1996) lists, for the mate-choice hypothesis, the following predictions: (1) the form of assortative mating will be true, (2) mating males will be larger than nonmating males, and (3) mating females will be larger than nonmating females. The first prediction has been tested (Bernstein and Bernstein 1998) and found true: the correlation between body sizes of mates is true (linear) rather than apparent (in which the variance in male size changes with increasing female size). Here, we test the remaining 2 predictions, specifically that mating individuals are larger than nonmating individuals in the populations that exhibit assortative mating but not in the populations that do not exhibit assortative mating.

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METHODS

We collected mating and nonmating beetles from 2 sites, one on the plains and the other in a canyon, within 30 km of Boulder, Colorado. The plains site is a meadow (elevation 1760 m) near Eldorado Springs, where beetles were feeding and mating on sunflower (*Helianthus annuus* L.) blossoms. The canyon site is a roadside in South St. Vrain Canyon (elevation 1830 m) near Lyons, where beetles were feeding and mating on blossoms of rabbitbrush [*Chrysothamnus nauseosus* (Pall.) Britt.]. Each sampling site encompassed an area of less than 0.5 ha. At each site 4 samples were taken at 1-wk intervals during the approximately month-long mating season. All beetles in each sample were collected on a single morning, between 0900 h and 1030 h. At this time of day beetles are too cool for rapid locomotion and so are likely to have been coupled since at least the previous evening. The sluggish condition also prevents sampling bias, as any beetle (regardless of size or mating status) is easily captured by sliding it from a blossom into a collecting vial. Whenever possible, each sample consisted of 40 mating pairs, 40 nonmating males, and 40 nonmating females. Samples of mating pairs are the same ones reported in an earlier publication in which patterns of assortative mating were described (Bernstein and Bernstein 1998).

Beetles were frozen within a few hours after capture and then preserved in 70% alcohol. Plains samples consisted entirely of *Chauliognathus basalis.* Canyon samples consisted of 2 species, *Chauliognathus deceptus* and *C. basalis*, an unexpected result since the 2 species cannot be distinguished in the field. Males were identified to species by the shape of the copulatory organ, using the key provided in Fender (1964); females were identified by species-specific correlations between length of the posterior elytron spot and length of the elytron (Bernstein and Bernstein 1998). The right elytron of each beetle was severed from the body and its maximum length was measured to the nearest 0.001 mm, using a binocular microscope with an eyepiece micrometer.

The effects of sampling time and mating status (mating versus nonmating) on body size were analyzed by 2-factor analyses of variance. Sampling time represents both progression of the mating season and variations in assortative mating, as only the first 2 samples at the canyon site exhibited this mating pattern (Bernstein and Bernstein 1998). All samples were reduced in size (by random elimination) to the smallest sample in order to meet the recommended equal sample sizes for the 2-factor ANOVA. We began with 24 groups: a male group and a female group from each of the 4 samples of *C. deceptus* at the canyon site, from each of the 4 samples of *C. basalis* at the canyon site, and from each of the 4 samples of *C. basalis* at the plains site. Five of the 24 groups were eliminated from analysis, 4 because they were too small (the male group and female group from samples 3 and 4 of *C. basalis* at the canyon site) and 1 because it was so much smaller than the other samples (sample 4 of *C. basalis* females at the plains site) that we preferred to eliminate it rather than greatly reduce the other samples. Where significant effects of sampling time were found, the means of mating and of nonmating individuals were compared using the Newman-Keuls multiple-comparison test (Zar 1996) with the level of significance set at 0.05.

In presenting a summary of our results, we compare the pattern of assortative mating with the pattern of size differences between mating and nonmating individuals among the samples. Part of this comparison involved testing for differences among the Pearson product correlation coefficients (*r*), our measure of assortative mating. For these tests we followed the statistical procedures described by Zar (1996) with the level of significance set at 0.05.

TABLE 1. Two-factor ANOVA results for males: effects of sampling time and mating status (mating versus nonmating) on elytron length (NS = $P > 0.05$; NA = not applicable).

Species (site)	Effect of sampling time	Effect of mating status	Interaction effect	Newman-Keuls test ($P < 0.05$)
C. deceptus (canyon)	$F_{3,216} = 4.270$ ($P < 0.01$)	$F_{1,216} = 16.050$ ($P < 0.0005$)	$F_{3,216} = 4.981$ ($P < 0.0025$)	Mating: $\bar{x}_1 = \bar{x}_2 = \bar{x}_3 = \bar{x}_4$ Nonmating: $\bar{x}_1 = \bar{x}_2 > \bar{x}_3 = \bar{x}_4$
C. basalis (canyon)	$F_{1,36} = 0.380$ (NS)	$F_{1,36} = 1.264$ (NS)	$F_{1,36} = 0.157$ (NS)	NA
C. basalis (plains)	$F_{3,240} = 0.239$ (NS)	$F_{1,240} = 34.476$ ($P < 0.0005$)	$F_{3,240} = 0.221$ (NS)	NA

TABLE 2. Two-factor ANOVA results for females: effects of sampling time and mating status (mating versus nonmating) on elytron length (NS = $P > 0.05$; NA = not applicable).

Species (site)	Effect of sampling time	Effect of mating status	Interaction effect	Newman-Keuls test ($P < 0.05$)
C. deceptus (canyon)	$F_{3,176} = 4.752$ ($P < 0.005$)	$F_{1,176} = 30.827$ ($P < 0.0005$)	$F_{3,176} = 8.474$ ($P < 0.0005$)	Mating: $\bar{x}_1 = \bar{x}_2 = \bar{x}_3 = \bar{x}_4$ Nonmating: $\bar{x}_1 = \bar{x}_2 > \bar{x}_3 = \bar{x}_4$
C. basalis (canyon)	$F_{1,36} = 0.124$ (NS)	$F_{1,36} = 0.270$ (NS)	$F_{1,36} = 0.108$ (NS)	NA
C. basalis (plains)	$F_{2,234} = 0.014$ (NS)	$F_{1,234} = 15.410$ ($P < 0.0005$)	$F_{2,234} = 0.534$ (NS)	NA

RESULTS

Results of the 2-factor analyses of variance are presented for males in Table 1 and females in Table 2. Each table shows the effect on mean elytron length of sampling time, mating status, and interaction between sampling time and mating status. Results of the Newman-Keuls test for differences among sampling times are provided for each ANOVA with a significant difference among samples.

Males and females exhibit the same ANOVA pattern. In *C. deceptus* there are significant effects of sampling time and mating status, as well as the interaction between sampling time and mating status, on elytron lengths. An interaction effect indicates that size differences between mating and nonmating individuals occur in some samples but not in others. According to the Newman-Keuls multiple-comparisons tests, elytron lengths of mating individuals remain the same across samples, whereas in nonmating individuals there is a significant difference between samples 2 and 3 (i.e., nonmating individuals are smaller in samples 3 and 4 than in samples 1 and 2). For *C. basalis* at the canyon site (samples 1 and 2), there are no effects of sampling time, mating status, or interaction on the elytron length of either males or females. For *C. basalis* at the plains site, there is a significant effect of mating status on elytron length but no effect of sampling time nor of an interaction (i.e., mating and nonmating individuals are different in size, and this difference remains the same across samples).

Results of our studies are summarized in Table 3 where, for each sample, we give the relative abundance of a congener, correlation coefficient (r) of elytron lengths of mating pairs, size ratio of mating to nonmating males, and size ratio of mating to nonmating females. For both species, samples 1 and 2 from the canyon site have higher correlation coefficients, higher percentages of the less abundant species, and virtually no size differences between mating and nonmating individuals. For *C. deceptus* in samples 3 and 4 from the canyon site and for all *C. basalis* samples from the plains site, correlation coefficients are low, percentages of the less abundant species are low, and mating and nonmating individuals are more different in size than in samples 1 and 2 from the canyon. There are significant

TABLE 3. Summary of sample values: percent of the less abundant species (n = total number of individuals in the sample), strength of assortative mating (coefficient r of the correlation between elytron lengths of mates; n = number of pairs), and size ratios of mated and unmated individuals (n = number of ratios = n of groups in the ANOVA).

	Sample 1	Sample 2	Sample 3	Sample 4
C. deceptus (canyon site)				
% less abundant species in sample	29.4 (n = 160)	32.5 (n = 160)	10.6 (n = 160)	13.1 (n = 160)
r values (differences among the values: $P < 0.05$)	0.421 (n = 30)	0.651 (n = 28)	0.157 (n = 38)	–0.019 (n = 36)
male size ratio: mated ÷ unmated	1.000 (n = 28)	1.002 (n = 28)	1.057 (n = 28)	1.064 (n = 28)
female size ratio: mated ÷ unmated	1.006 (n = 23)	1.001 (n = 23)	1.087 (n = 23)	1.067 (n = 23)
C. basalis (canyon site)				
% less abundant species in sample	29.4 (n = 160)	32.5 (n = 160)	10.6 (n = 160)	13.1 (n = 160)
r values (differences among the values: NS)	0.533 (n = 10)	0.529 (n = 12)	too few	too few
male size ratio: mated ÷ unmated	1.022 (n = 10)	1.013 (n = 10)	too few	too few
female size ratio: mated ÷ unmated	1.003 (n = 10)	1.015 (n = 10)	too few	too few
C. basalis (plains site)				
% less abundant species in sample	0 (n = 160)	0 (n = 160)	0 (n = 160)	0 (n = 124)
r values (differences among the values: NS)	0.042 (n = 40)	0.095 (n = 40)	0.168 (n = 40)	–0.088 (n = 40)
male size ratio: mated ÷ unmated	1.048 (n = 31)	1.042 (n = 31)	1.047 (n = 31)	1.033 (n = 31)
female size ratio: mated ÷ unmated	1.039 (n = 40)	1.037 (n = 40)	1.020 (n = 40)	too few

differences (χ^2 = 9.571) among correlation coefficients (r) of the 4 samples of *C. deceptus* at the canyon site. There is no significant difference (z = 0.011) between correlation coefficients of the 2 samples of *C. basalis* in the canyon, nor are there significant differences (χ^2 = 0.309) among the 4 samples of *C. basalis* in the plains site.

DISCUSSION

One hypothesis to explain positive assortative mating is the mate-choice hypothesis in which individuals prefer larger mates. A prediction of this hypothesis (in addition to assortative mating) is that mating individuals are larger than nonmating individuals because larger individuals mate more often and/or remain coupled for longer periods of time than the less desirable, smaller individuals. We tested the specific prediction that mating individuals are larger than nonmating individuals in populations that exhibit positive assortative mating and found the prediction to be false for 2 species of soldier beetles (*C. basalis* and *C. deceptus*). In populations of these species that exhibit assortative mating (as measured by corrrelations of the elytron lengths of mates), there are no differences between elytron lengths of mating and nonmating individuals. In populations that do not exhibit assortative mating, however, mating males and females are larger than nonmating males and females.

Is mate choice the usual mating pattern in soldier beetles? Where mate choice (as defined by larger mating than nonmating individuals) was examined in previous studies, all involving *C. pennsylvanicus*, the results were mixed. Mason (1980) found evidence of female choice (larger mating than nonmating males) in 2 of 3 populations sampled in northern New York, but no evidence of male choice. McLain (1982) found both male and female choice in all 6 populations sampled in northern Georgia. A later study (McLain 1985) found no evidence of female choice (only males were measured) in a cline of 15 populations in northern Georgia.

A tentative interpretation of our results is that mate choice is the normal mating pattern in soldier beetles, but that presence of a congener on the same host plant inhibits this normal behavior and triggers assortative mating. What is the evidence that assortative mating and mate choice are alternative mating patterns in soldier beetles? Three previous studies, all involving *C. pennsylvanicus*, have evaluated both mating patterns in the same populations. McLain (1982) found both male and female choice, but no asssortative mating, in 6 populations he sampled in Georgia (a result that lends support to our interpretation). However, in a later study McLain (1985) found neither mate choice nor assortative mating in a cline of 15 populations in Georgia. McCauley and Wade (1978) found both mate choice (by males and by females) and assortative mating in populations they studied in Illinois. Thus, the results on *C. pennsylvanicus* do not form a consistent pattern.

Our results suggest that the soldier beetles we studied exhibit mate-choice behavior except in the presence of a congener. McLain (1981), in studies of *C. pennsylvanicus*, also found inhibition of mate-choice behavior (in females) by the presence of other species, in this case wasps. Wasps were less aggressive toward pairs of beetles than toward individuals, so that paired females were able to feed more efficiently than unpaired females. Thus, the advantage of mating with a larger male is countered by the advantage of being paired, regardless of mate size, under these conditions. In our study the advantage of having a large mate may be countered by the disadvantage of mating with an individual of the wrong species. The relationship between inhibition of mate choice and stimulation of assortative mating, however, remains unclear.

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BODY SIZE DYNAMICS OF COUGARS (*FELIS CONCOLOR*) IN OREGON

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Key words: Felis concolor, *Oregon, body mass.*

We investigated body size dynamics of 1076 harvested male and female cougars in Oregon from 1987 through 1997. Cougars were checked, weighed, and measured by Oregon Department of Fish and Wildlife biologists within 48 h of harvest. One or 2 upper premolars were removed and age was determined by cementum annuli at Matson's Lab (Milltown, MT). Precision of age determination was estimated from 864 "blind tests" of pairs of premolars for which the identity of the individual cougar was not known to the analyzing laboratory personnel. Ages assigned to each of the 2 premolars agreed exactly or varied by 1 yr in 93% of the <4-yr-old cougars, while 54% of the premolar pairs of older cougars were the same age or differed by 1 yr.

Body length (BL, nose-to-tip-of-tail) and body mass (BM) were significantly correlated for both sexes (males: $BL = 145.67 + 1.073BM$, $n = 645$, $F = 1123.7$, $P < 0.0001$, $R^2 = 0.63$; females: $BL = 123.66 + 1.68BM$, $n = 431$, $F = 596.4$, $P < 0.0001$, $R^2 = 0.58$). Mean body mass of male cougars was, on average, 50.8% (±14.2%) greater than that of females. This difference was statistically significant for all age classes except kittens (Table 1) and supports results from earlier studies

TABLE 1. Mean body mass (kg), standard error, and sample size of harvested male and female cougars in Oregon, 1987–1997. Asterisks indicate significant differences in body mass between the sexes ($P < 0.05$). Significant differences among seasonal mass within age groups are represented by different superscript letters (Tukey test, $P < 0.05$).

Sex	Age	Jun–Aug $(\bar{x} \pm s_{\bar{x}}, n)$	Sep–Nov $(\bar{x} \pm s_{\bar{x}}, n)$	Dec–Feb $(\bar{x} \pm s_{\bar{x}}, n)$	Mar–May $(\bar{x} \pm s_{\bar{x}}, n)$	Total $(\bar{x} \pm s_{\bar{x}}, n)$
Male	0	20.0 ± 4.4, 6	17.1 ± 3.8, 7	22.6 ± 1.5, 18	15.0 ± 1.4, 8	19.7 ± 1.3, 39
	1	37.3 ± 2.0, 18	43.4 ± 1.8, 18	43.8 ± 1.8, 32	44.0 ± 3.0, 8	42.2 ± 1.1, 76*
	2	38.1 ± 3.2, 8^{a}	49.0 ± 1.3, 40^{b}	50.6 ± 0.8, 83^{b}	46.0 ± 2.4, 9^{a}	49.1 ± 0.7, 140*
	3	52.1 ± 2.3, 6^{a,b}	56.8 ± 1.5, 21^{a,b}	57.2 ± 1.0, 71^{a}	49.6 ± 3.2, 11^{b}	56.1 ± 0.8, 109*
	4	55.3 ± 3.2, 7	58.8 ± 1.3, 18	59.6 ± 1.0, 54	57.9 ± 2.8, 11	58.9 ± 0.8, 90*
	5	55.0 ± 3.3, 4	59.4 ± 1.6, 16	60.3 ± 1.1, 46	56.8 ± 2.3, 2	59.7 ± 0.9, 68*
	6	57.3 ± 6.0, 4	60.0 ± 1.8, 16	62.2 ± 1.1, 54	53.8 ± 2.0, 3	61.2 ± 0.9, 77*
	7	54.5 ± 0, 1	61.4 ± 3.0, 6	65.5 ± 1.5, 25	63.6 ± 0, 1	64.4 ± 1.3, 33*
	8	61.6 ± 1.6, 2	73.6 ± 5.9, 3	63.6 ± 1.9, 16	63.6 ± 0, 1	64.8 ± 1.7, 22*
	9	63.1 ± 8.8, 4	65.5 ± 2.6, 4	64.2 ± 3.1, 9	68.0 ± 2.6, 3	64.8 ± 2.2, 20*
	10 +	71.8 ± 0, 1	71.2 ± 2.0, 3	66.7 ± 1.8, 23	61.4 ± 0, 1	67.2 ± 1.6, 28*
Female	0	14.3 ± 1.9, 4	15.7 ± 2.1, 11	18.0 ± 1.7, 16	18.7 ± 2.1, 11	17.2 ± 1.0, 42
	1	28.4 ± 3.1, 7^{a,b}	33.6 ± 1.1, 21^{a}	31.9 ± 1.1, 28^{a,b}	27.7 ± 1.4, 13^{b}	31.3 ± 0.7, 69*
	2	31.5 ± 3.4, 3^{a,b}	36.1 ± 0.7, 26^{a,b}	36.9 ± 0.6, 65^{a}	32.5 ± 2.0, 12^{b}	36.0 ± 0.5, 106*
	3	31.8 ± 0, 1	38.1 ± 1.3, 18	37.2 ± 0.9, 41	34.4 ± 2.4, 3	37.2 ± 0.7, 63*
	4	—	38.4 ± 2.2, 10	39.1 ± 0.7, 34	38.9 ± 1.9, 6	39.0 ± 0.7, 50*
	5	29.1 ± 0, 1	40.4 ± 2.2, 7	39.9 ± 0.7, 32	31.8 ± 9.1, 2	39.3 ± 0.8, 42*
	6	40.9 ± 0, 1	42.8 ± 1.3, 8	39.0 ± 0.8, 20	35.5 ± 0, 1	40.0 ± 0.7, 30*
	7	35.0 ± 0, 1	43.5 ± 2.5, 5	41.8 ± 1.0, 11	45.0 ± 0, 1	42.0 ± 1.0, 18*
	8	—	47.7 ± 0, 2	40.9 ± 1.5, 10	—	42.0 ± 1.5, 12*
	9	—	48.2 ± 0, 1	41.5 ± 1.1, 11	35.9 ± 0, 1	41.6 ± 1.2, 13*
	10 +	35.9 ± 7.3, 2	43.6 ± 0.5, 2	40.9 ± 1.1, 16	45.0 ± 0, 2	41.1 ± 1.0, 22*

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(Anderson 1983). Body mass of subadult cougars increased rapidly until 4 yr of age, after which annual weight gain increments were less than 1% (Table 1).

Body mass of harvested cougars varied among seasons (Table 1), but significant seasonal mass changes occurred only in subadults. Young cougars experienced significant weight losses in spring and summer of their 2nd yr. Hornocker (1970) suggested that young cougars at the time of dispersal are vulnerable to starvation and accidental mortalities. We conclude that cougars in Oregon are highly sexually dimorphic and speculate that significant weight changes in subadults are a result of food deprivation during dispersal.

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HELMINTHS OF THE LOWLAND BURROWING TREEFROG, *PTYERNOHYLA FODIENS* (HYLIDAE), FROM SOUTHERN ARIZONA

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Key words: Pternohyla fodiens, *Hylidae, helminths, Arizona.*

The lowland burrowing treefrog, *Pternohyla fodiens* Boulenger, 1882, occurs from Pima County, Arizona, south into western México. In México it is found from Sonora to Michoacán at elevations from sea level to about 1490 m (Stebbins 1985). There are no published accounts of helminths from this species. The purpose of this note is to report the helminths of *Pternohyla fodiens* from southern Arizona and to list the other anuran species in which these helminths occur.

Forty *Pternohyla fodiens* (9 females, 31 males; mean snout-vent length = 55.1 mm, 2.9 *s*, range 45–70 mm) collected 3.5 km E of Sells, Pima County, Arizona (31°55′N, 111°55′W; elevation ca 2300 m) during 1958–1962 were borrowed from the herpetology collection of the University of Arizona, Tucson (UAZ numbers: 16141–16155, 16161–16164, 16166, 16200–16204, 16206–16208, 16212, 16240, 16258, 16261, 16908–16913, 16915, 16918). The treefrogs were originally fixed in 10% formalin and preserved in 70% isopropanol. The body cavity was opened, gastrointestinal tract removed, and the esophagus, stomach, small intestine, and large intestine were cut open and the contents examined. In addition, the lungs and bladder were searched for helminths. Nematodes were identified utilizing the glycerol wet-mount procedure. Cestodes were stained with hematoxylin and mounted in Canada balsam for identification. Terminology usage is in accordance with Bush et al. (1997).

The helminth fauna of *Pternohyla fodiens* consisted of 1 species of cestode, *Distoichometra bufonis* Dickey, 1921, and 5 species of nematodes: *Aplectana itzocanensis* Bravo Hollis, 1943, *Cosmocercella haberi* Steiner, 1924, *Rhabdias americanus* Baker, 1978, *Physaloptera* sp. (larva only), and *Skrjabinoptera* sp. (larvae only). Number of helminths, prevalence, mean intensity, range, mean abundance, and infection site are given in Table 1. Selected helminths were placed in vials of ethanol and deposited in the U.S. National Parasite Collection, Beltsville, Maryland: *Distoichometra bufonis* 87748, *Aplectana itzocanensis* 87749, *Cosmocercella haberi* 87750, *Rhabdias americanus* 87751, *Physaloptera* sp. 87752, *Skrjabinoptera* sp. 87753.

None of the helminths found during this study was unique to *Pternohyla fodiens*. *Distoichometra bufonis* has been reported previously from 6 anurans from Arizona: *Bufo cognatus*, *B. microscaphus*, *B. punctatus*, *B. retiformis*, *B. woodhousii*, and *Scaphiopus couchii* (Goldberg and Bursey 1991a, 1991b, Goldberg et al. 1996b, 1996c). It also has been reported from *Bufo boreas* from California, *B. cognatus* from New Mexico and Oklahoma, *B. terrestris* from Georgia, *B. woodhousii* from Nebraska, and *Hyla regilla* from Oregon (Dickey 1921, Kuntz 1941, Douglas 1958, Koller and Gaudin 1977, Hardin and Janovy 1988, Goldberg et al. 1995). Because *Distoichometra bufonis* has a wide distribution in North America, its occurrence in *Pternohyla fodiens* is not unexpected. It is a new host record.

Aplectana itzocanensis has been reported from 7 anurans from Arizona: *Bufo alvarius*, *B. cognatus*, *B. microscaphus*, *B. punctatus*, *B. retiformis*, *B. woodhousii*, and *Gastrophryne olivacea* (Goldberg and Bursey 1991a, 1991b, Goldberg et al. 1996b, 1996c, 1998). Additionally, it has been reported from *Bufo cognatus* from New Mexico, and *B. marinus* from Costa Rica and México (Bravo Hollis 1943, Brenes

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TABLE 1. Helminths from *Pternohyla fodiens* ($N = 40$) from southern Arizona.

Helminth	N	Prevalence (%)	Mean intensity ± s (range)	Mean abundance ± s	Site
CESTODA					
Distoichometra bufonis	7	8	2.3 ± 2.3 (1–5)	0.18 ± 0.81	small intestine
NEMATODA					
Aplectana itzocanensis	110	18	15.7 ± 36.7 (1–99)	2.75 ± 15.6	intestines
Cosmocercella haberi	2587	55	117.6 ± 126.1 (2–504)	64.68 ± 109.86	intestines
Rhabdias americanus	6	6	6.0	0.15 ± 0.95	lung
Physaloptera sp. (larvae)	7	7	1.8 ± 0.5 (1–2)	0.18 ± 0.55	stomach
Skrjabinoptera sp. (larva)	1	1	1.0	0.03 ± 0.16	stomach

and Bravo Hollis 1959, Caballero Deloya 1974, Baker 1985, Goldberg et al. 1995). The known distribution of *Aplectana itzocanensis* suggests it may be a Middle American species that reaches its northern distribution in the southwestern deserts of the United States. Its occurrence in *Pternohyla fodiens* is a new host record.

Cosmocercella haberi has been reported from 2 anurans from Arizona, *Hyla arenicolor* and *H. wrightorum* (Goldberg et al. 1996a), as well as *H. arenicolor* from Utah, *H. cinerea* from North Carolina, and *H. versicolor* from Virginia and Ontario, Canada (Steiner 1924, Parry and Grundmann 1965, Campbell 1968, Baker and Adamson 1977). Parry and Grundmann (1965) reported 1 of 23 *Rana pipiens* from Utah to be infected by *Cosmocercella haberi*, the only report of infection of a nonhylid species. Because of its wide distribution as a parasite of hylids, its occurrence in *Pternohyla fodiens* is not unexpected. It is a new host record.

Rhabdias americanus has been reported from 5 anurans from Arizona: *Bufo alvarius*, *B. cognatus*, *B. microscaphus*, *B. retiformis*, and *B. woodhousii* (Goldberg and Bursey 1991a, Goldberg et al. 1996b, 1996c). It has also been reported from *B. americanus* and *B. woodhousii* from eastern North America and Canada (Baker 1978) and *B. cognatus* from New Mexico (Goldberg et al. 1995). This is the first report of *Rhabdias americanus* in an anuran other than a bufonid and its occurrence in *Pternohyla fodiens* is a new host record.

Species of *Physaloptera* require insects as an intermediate host, while species of *Skrjabinoptera* require ants as an intermediate host (Anderson 1992). Since only larvae were found in this study, we assumed that *Pternohyla fodiens* is an unsuitable host and that the appearance of larvae from these 2 genera is the result of treefrog diet rather than a normal part of the parasite's life cycle. To our knowledge, no case of adult physalopterans in anurans of North America has been reported. Any insectivore could be expected to have larvae of these 2 genera.

In summary, *Pternohyla fodiens* was found to harbor 1 species of cestode and 3 species of nematodes which also occur in other anurans of North America. *Pternohyla fodiens* is a new host record for each of these species. Examination of samples of *P. fodiens* from the southern part of its range in México will be necessary before the diversity of parasitic helminths in this hylid can be known.

We thank Charles H. Lowe, Department of Ecology and Evolutionary Biology, University of Arizona, for permission to examine specimens of *Pternohyla fodiens*.

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HELMINTHS OF THE MADREAN ALLIGATOR LIZARD, *ELGARIA KINGII* (SAURIA: ANGUIDAE), FROM ARIZONA

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Key words: Elgaria kingii, *Anguidae, helminths, Arizona.*

The Madrean alligator lizard, *Elgaria kingii* Gray, 1838, occurs from the southern edge of the central plateau of Arizona southward in the Sierra Madre of México to Jalisco, México; it frequents chaparral, oak woodland, and pine-fir forests and occurs from 760 to 2070 m (Stebbins 1985). There are no accounts of helminths from this species. The purpose of our paper is twofold: to provide the first report of helminths from *E. kingii* collected in Arizona and to furnish a list of parasites known from the genus *Elgaria.*

We borrowed 31 *E. kingii* from Arizona from the herpetology collection of the University of Arizona (UAZ), Tucson (mean snout-vent length, 68 mm, 8.2 *s*, range 48–80 mm). The lizards were originally preserved in 10% formalin and stored in 70% isopropanol. Specimens examined are listed by county of collection in Appendix 1. The body cavity was opened and the gastrointestinal tract excised by cutting across the esophagus and rectum. The esophagus, stomach, and small and large intestines were slit longitudinally and examined separately under a dissecting microscope. The body cavity and liver surface were also examined. Each helminth was removed to a temporary glycerol mount for examination. Nematodes were identified from these temporary mounts. Cestodes were stained in hematoxylin and mounted in Canada balsam for identification. Voucher specimens were deposited in the U.S. National Parasite Collection (Appendix 2). Terminology usage is in accordance with Bush et al. (1997).

Elgaria kingii harbored 2 species of cestodes, *Mesocestoides* sp. (tetrathyridia) and *Oochoristica eumecis* Harwood, 1932, and 4 species of nematodes: *Cosmocercoides variabilis* (Harwood, 1930) Travassos, 1931, *Spauligodon goldbergi* Bursey and McAllister, 1996, *Physaloptera* sp. (larvae), and *Skrjabinoptera* sp. (larvae). Prevalence, mean intensity, range and mean abundance are given in Table 1. *Elgaria kingii* is a new host record for each helminth species.

None of the helminths found in this study was unique to *Elgaria kingii.* Gravid individuals of the following 3 species were found. *Oochoristica eumecis* was originally described from the skink, *Eumeces fasciatus,* from Texas (Harwood 1932) and has been reported from *Ctenosaura pectinata* from México (Flores-Barroeta et al. 1958); *E. kingii* is the 3rd host record. *Cosmocercoides variabilis* is known from a variety of amphibians and reptiles from North America (Baker 1987); *E. kingii* represents the 26th host record. *Spauligodon goldbergi* was originally described from the ground snake, *Sonora semiannulata,* from central Texas by Bursey and McAllister (1996); *E. kingii* is the 2nd host record.

Three species of helminths were represented by immature forms. Tetrathyridia of *Mesocestoides* sp. occur commonly in the coleomic cavities of lizards and snakes which are considered to be paratenic hosts (Bolette 1997). Adults of *Physaloptera* and *Skrjabinoptera* are frequently seen gastric parasites of lizards (Baker 1987). Because only 3rd-stage larvae of these 2 genera were found, their importance to the helminth load of *E. kingii* cannot be assessed.

Parasite lists (Table 2) can now be developed for 3 of 4 species of *Elgaria* occurring in North America, namely, *E. coerulea, E. kingii,* and *E. multicarinata; E. panamintina* has not yet been examined. There is some overlap in

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TABLE 1. Helminths from *Elgaria kingii* ($N = 31$) from Arizona.

Helminth	N	Prevalence (%)	Mean intensity ± s (range)	Mean abundance ± s	Site
CESTODA					
Mesocestoides sp. (tetrathyridia)	47	3	47.0	1.52 ± 8.44	coelom
Oochoristica eumecis	1	3	1.0	0.03 ± 0.18	small intestine
NEMATODA					
Cosmocercoides variabilis	8	13	2.0 ± 2.0 (1–5)	0.26 ± 0.93	large intestine
Spauligodon goldbergi	40	10	13.3 ± 10.2 (6–25)	1.29 ± 4.79	small, large intestines
Physaloptera sp. (larvae)	34	35	3.1 ± 3.2 (1–11)	1.10 ± 2.39	stomach, small, large intestines
Skrjabinoptera sp. (larvae)	36	6	18.0 ± 18.3 (5–31)	1.16 ± 5.61	stomach

TABLE 2. Prevalence of helminths in species of *Elgaria* from North America.

Species of *Elgaria* Helminth	Location	Prevalence	Reference
E. coerulea			
Mesocestoides sp. (tetrathyridia)	Contra Costa Co., CA	not given	Voge 1953
Cosmocercoides sp.	Whatcom Co., WA	2% (2/104)	Goldberg and Bursey 1991
Oswaldocruzia sp.	Whatcom Co., WA	1% (1/104)	Goldberg and Bursey 1991
E. kingii			
Mesocestoides sp. (tetrathyridia)	Gila Co., AZ	3% (1/31)	this study
Oochoristica eumecis	Santa Cruz Co., AZ	3% (1/31)	this study
Cosmocercoides variabilis	Cochise, Pima cos., AZ	13% (4/31)	this study
Spauligodon goldbergi	Cochise Co., AZ	10% (3/31)	this study
Physaloptera sp. (larvae)	Cochise, Graham, Pima cos., AZ	35% (11/31)	this study
Skrjabinoptera sp. (larvae)	Cochise Co., AZ	6% (2/31)	this study
E. multicarinata			
Baerietta gerrhonoti	Los Angeles Co., CA	64% (16/25)	Telford 1970
Mesocestoides sp. (tetrathyridia)	Riverside Co., CA	7% (2/30)	Telford 1970
Oochoristica sp.	Los Angeles Co., CA	1% (1/96)	Goldberg and Bursey 1990
Physaloptera retusa	Riverside Co., CA	13% (4/30)	Telford 1970
Physaloptera sp. (larvae)	Los Angeles Co., CA	1% (1/96)	Goldberg and Bursey 1990
Oswaldocruzia pipiens	Los Angeles Co., CA	2% (2/96)	Goldberg and Bursey 1990

the helminth genera harbored (Table 2), but too few helminths have been found to evaluate the helminth community in species of *Elgaria*. Except for the 64% (16/25) prevalence of the cestode *Baerietta gerrhonoti* reported by Telford (1965), prevalences of helminth species of *Elgaria* are low.

We thank Charles H. Lowe, Department of Ecology and Evolutionary Biology, University of Arizona, for permission to examine specimens of *Elgaria kingii* for helminths.

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APPENDIX 1

Museum accession numbers for specimens of *Elgaria kingii* (*N* = 31) from the University of Arizona (UAZ) listed by Arizona County. **Cochise** (UAZ 15501, 15691, 36871, 37918–37920, 39487, 39711, 39715, 40032–40033, 40308, 40938–40939, 40941–40942, 40944, 40947, 46845, 47297, 48012); **Gila** (UAZ 36731, 40309); **Graham** (UAZ 36362, 39710, 43862); **Pima** (UAZ 11248, 19773–19774) **Santa Cruz** (UAZ 11990, 49171).

APPENDIX 2

Accession numbers for helminths of *Elgaria kingii* deposited in the U.S. National Parasite Collection. *Mesocestoides* sp. (87667), *Oochoristica eumecis* (87664), *Cosmocercoides variabilis* (87665), *Spauligodon goldbergi* (87666), *Physaloptera* sp. (87668), *Skrjabinoptera* sp. (87669).

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C[HARLES] LYNN HAYWARD

Herbert H. Frost[1] and Wilmer W. Tanner[1]

Dr. C. Lynn Hayward, professor emeritus of zoology and entomology, Brigham Young University, Provo, Utah, died 30 August 1998. He was born 10 July 1903 in Paris, Idaho, where he spent his early years, graduating from Fielding High School in 1923. Later that same year Lynn entered Brigham Young University, receiving a B.S. degree in 1927. Following his university experience he returned to his hometown in Idaho and taught biology and English at the high school for 3 years. In May 1930 he returned to BYU on an assistantship in the Zoology and Entomology Department. On 6 August 1930 he married Elizabeth (Libbie) Cook. To them were born 2 children, Margaret and Gerald.

In 1931 he completed his master's degree in entomology at BYU and became a zoology instructor there. Lynn Hayward entered BYU as the Department of Zoology was being established, and though it was first designated as the Zoology and Entomology Department, his role was to establish and teach basic zoological classes pertaining to vertebrates. From 1931 to 1942 he taught in the department and, during the beginning years, began research in preparation for a doctoral degree. In 1935 he did graduate work at the University of California at Berkeley and in 1941 completed his dissertation in ecology at the University of Illinois under Professor Victor Shelford, one of the pioneer ecologists. His Ph.D. graduate studies emphasized systematics and ecology of birds and mammals.

C. Lynn Hayward

During his early teaching years at Fielding High School, Lynn made a collection of 94 bird skins and several sets of eggs. These eventually became the nucleus of BYU's ornithological collection, which now numbers 9551 bird skin specimens and 9000 sets of eggs. Because of his collecting background, Lynn assumed the position of curator of the bird and mammal collections at BYU. In the early 1930s, with the Depression in full force, equipment funds were limited. Having been raised in a rural community, he knew how to work with his hands and so obtained plans for the construction of bird and mammal cases and built several for the growing collections. Today the mammal collection contains 15,621 skins and whole mount specimens.

Lynn had a good grasp of the English language. Thus, his lectures and research writings were clear and meaningful. He engaged his students in biological field studies that required careful observations and ecological evaluations of the environment. Many of his field classes involved preparing bird and mammal skins; as the students became proficient in mounting, their best specimens became part of the university's collections.

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He was always willing to work with his students and his door was open for them to come to him for advice. He chaired 18 students' graduate committees and was a member for many more. His graduate students were well trained and have become recognized in their fields. His research is best seen in two publications, "Biotic communities of the Wasatch chaparral" and "Alpine biotic communities of the Uinta Mountains, Utah." His "Bibliography of the mammals of Utah" and "Birds of Utah" have been used and will continue to be used as resource materials by many who are conducting research in vertebrate zoology of western North America.

In addition to his teaching and research, Lynn had, over the years, a number of administrative responsibilities at BYU. For 7 years he served on the admission and credits committee, a year on the curriculum committee, and many years as chair of the premedical and predental committee. He chaired the Zoology Department from 1958 to 1962 and was, for 5 years, curator of the Life Science Museum, which was the forerunner of the Monte L. Bean Museum. On 30 August 1974 he was presented the BYU Alumni Distinguished Service Award for teaching and research. During his professional years he wrote and collaborated on 147 articles. The following 42 papers, covering a 53-year period, are considered to be his most important contributions.

1. 1930 Notes on Utah Vespidae. Entomological News 41:204–205, 222–226.
2. 1931 A preliminary list of the birds of the subalpine and alpine zones of the Uinta Mountains. Utah Academy of Science 8:151–152.
3. 1932 The paper wasps of Utah including a description of a new variety of *Polistes canadensis* Linn. Utah Academy of Science 9:85–101.
4. 1933 Notes on the taxonomy and description of the wasp genus *Polistes* in the Intermountain West, with description of two new varieties. Utah Academy of Science 10:139–147.
5. 1933 Distribution of *Polistes* in Canada, with notes on the genus (Hymenop.). Canadian Entomologist 65:126–128.
6. 1934 Important heron rookeries in southeastern Idaho. Auk 51:39–41.
7. 1934 A biological study of the La Sal Mountains. Utah Academy of Science 11:209, 235 (with V.M. Tanner).
8. 1935 The breeding status and migration of the Caspian Tern in Utah. Condor 37:140–144.
9. 1935 Observations on some breeding birds of Mount Timpanogos, Utah. Wilson Bulletin 47:161–162.
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13. 1937 A record of *Vespa crabro* Linnaeus from North Dakota. Entomological News 48:120.
14. 1937 Some new and unusual bird records from Utah. Wilson Bulletin 69:303–305.
15. 1940 Notes on the distribution of nighthawks in Utah. Great Basin Naturalist 1:93–96.
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17. 1941 Notes on the nesting habits of some mountain dwelling birds in Utah. Great Basin Naturalist 2:1–8.
18. 1941 Three new mammals (*Microtus* and *Ochotona*) from Utah. Great Basin Naturalist 2:105–108 (with E.R. Hall).
19. 1941 A bibliography of Utah mammalogy: including references to names and type localities (first supplement). Great Basin Naturalist 2: 125–136.
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14–16 October 1999

University of Nevada, Reno

The University of Nevada, Reno will host the first Great Basin Biological Research Conference 14–16 October 1999. The conference will feature contributed presentations and posters, keynote speakers, and roundtable discussions related to the biological study and management of the Great Basin and eastern Sierra Nevada ecoregions. Also, several field trips have been planned.

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EFFECTS OF HABITAT TYPE AND DEGRADATION ON AVIAN SPECIES RICHNESS IN GREAT BASIN RIPARIAN HABITATS

Ian G. Warkentin[1] and J. Michael Reed[2]

Abstract.—The overwhelming majority of bird species in the Great Basin region are found in riparian habitats. However, most previous research on the impact of change in habitat condition through degradation on these bird communities failed to account for the large intersite differences in both habitat type and extent of degradation. We examined songbird communities in 4 riparian habitat types (meadows, willow-, birch-, and aspen-dominated forest stands) during summers 1994 (last year of a 7-yr drought) and 1995 (following the 6th wettest winter recorded) in the Toiyabe Mountain Range of central Nevada. Habitat degradation significantly influenced bird species richness in riparian areas, but the impact was dependent upon habitat type. While meadow bird communities were affected adversely by habitat degradation, with significant drops in species richness on degraded sites, bird species richness in forested riparian habitats was consistently greater on degraded sites. Data for the 6 most common species seen during our study indicated that degradation may have influenced distribution of American Robins (*Turdus migratorius*) and Yellow Warblers (*Dendroica petechia*), but habitat type was the best predictor of abundance for House Wrens (*Troglodytes aedon*), Red-naped Sapsuckers (*Sphyrapicus nuchalis*), Warbling Vireos (*Vireo gilvus*), and Brewer's Blackbirds (*Euphagus cyanocephalus*). Avian species diversity in meadow habitats may be linked to moisture levels during specific times of the year. Diversity increased during the pre-migratory period of the dry year (1994) when compared with that of the breeding season, but was unchanged in the wet year (1995).

Key words: riparian woodland, meadow, grazing, breeding, songbird, Nevada.

Riparian woodlands in western United States support some of the highest densities of breeding landbirds in the United States and Canada (Carothers et al. 1974, Knopf et al. 1988). Although such habitats cover <1% of the total regional landmass, 2/3 to 3/4 of regional, nongame landbird species are associated primarily with these riparian areas during the breeding season (reviewed in Saab et al. 1995). Riparian habitats are attractive to birds for a variety of reasons. Streams produce invertebrates that are the primary prey of many of these birds, and adjacent vegetation provides nest sites not otherwise available in the surrounding landscape (Ryser 1985).

Due to their strong dependence upon riparian areas, landbird communities in the Great Basin region may be affected by any activities altering habitat condition. Over the last decade concern about these limited riparian habitats has attracted increasing attention; one focal point has been the potential impact of livestock grazing (e.g., Knopf et al. 1988, Fleischner 1994, Knopf and Samson 1994, Brown and McDonald 1995, Saab et al. 1995). Water, shade, and diverse succulent vegetation of these riparian areas attract not only wildlife (e.g., Johnson et al. 1977, Thomas et al. 1979) but also grazing livestock (Gillen et al. 1984). Problems arise because riparian areas are highly susceptible to degradation by the concentrated activities of domesticated animals. Grazing livestock can substantially alter essential characteristics of streams by changing surrounding vegetative structure and species composition, altering soil structure and porosity, and modifying stream bank morphology (e.g., Smith 1940, Ellison 1960, Brown 1978, Platts 1981, Kauffman and Krueger 1984, Milchunas et al. 1988, Baker and Guthery 1990, Smith et al. 1994).

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Generalizing anticipated impacts of activities, such as grazing, on native flora and fauna can be difficult because riparian areas differ greatly among sites in such characteristics as plant community structure and extent of habitat degradation (Carothers et al. 1974, Rice et al. 1983). Summaries such as those of Saab et al. (1995), which pool data from numerous studies, are useful as an initial approximation of the impact of grazing on riparian avifauna across a wide range of habitat and degradation types, but must be applied with caution to specific sites.

Livestock grazing, one agent of change in these riparian systems, is the general context for this study. However, disturbance through grazing by native wildlife, droughts, floods, insect outbreaks, and wildfires also may alter habitat conditions. In this study we used techniques developed by the U.S. Forest Service (Weixelman et al. 1996; see Methods) to quantify the general condition of riparian forested habitats and meadows on the basis of soil and understory vegetation characteristics. We examined how habitat conditions, created by various disturbances listed above, affected bird communities in riparian habitats of central Nevada compared with communities found in relatively undisturbed riparian habitats of the same region. Although livestock grazing may have led to substantial change in parts of the study area, our main interest lay in the correlation between the general condition of riparian habitats and bird communities found in them, rather than a direct link between cattle grazing intensity and avian species richness.

We present results of census data for songbird communities from 4 different riparian habitat types, at known levels of habitat degradation, within a limited geographic area, in a replicated study conducted over 2 yr. Our objectives were to (1) determine whether observed levels of habitat degradation affected bird species composition (and abundance of the 6 most common species), and (2) determine if these effects differed among habitat types. In the case of meadow habitat, we also were interested in variation by period within the summer season.

STUDY AREA AND METHODS

Censuses were conducted over 2 summers in the Toiyabe Mountain Range, which is part of the Humboldt-Toiyabe National Forest located 240 km east of Reno in central Nevada, USA (Lander and Nye counties; 39°N, 117°W). This narrow, 200-km-long range is oriented north–south with peaks ranging in elevation from 2100 to 3600 m. Along its length are a large number of deep canyons with riparian areas seldom exceeding 30–50 m wide at stream level. Dominant vegetation in the canyons includes quaking aspen (*Populus tremuloides*), water birch (*Betula occidentalis*), willow (*Salix* spp.), and meadow plant assemblages (e.g., characterized by dense cover of *Carex nebrascensis*, *C. aquatilus*, *Poa secunda*, *Juncus balticus*, or *Deschampsia cespitosa*). Seasonal precipitation typically is less than 250 mm in basins on either side of the range, with about 60% falling in autumn and winter (Weixelman et al. 1996). Summer 1994 was the last year of a 7-yr drought, and summer 1995 followed the 6th wettest winter recorded for this region (data for Austin, NV, from the Western Regional Climate Center, Reno, NV). Indirect human disturbance of these canyons through cattle and sheep grazing at varying intensities has led to significant changes in vegetative structure and composition over recent times. Human recreational activities and natural disturbances such as droughts, floods, and wildfires also have resulted in some habitat degradation. We assessed the degradation level at each census site on the basis of soil and understory plant characteristics (see below).

General Censuses

We established 42 transects in 19 drainages along the range. The transects represented 4 riparian habitat types (meadow, willow, aspen and birch) at 2 levels of degradation (high and low). They included 9 moist meadows (5 on highly degraded sites and 4 on minimally degraded sites), 15 willow habitats (9 high and 6 low), 10 aspen habitats (7 high and 3 low), and 8 birch habitats (5 high and 3 low). These transects were assigned to plant communities and degradation types by the Humboldt-Toiyabe National Forest Ecology Team, using criteria described in detail by Weixelman et al. (1996). Soil, water, climate, and plant species present determined community assignment. Criteria for degradation level included factors such as seral stage association of plant species present, groundcover, extent of water infiltration, root depth and abundance, and soil temperature. Values for sites of each habitat type were compared with those of the potential natural community to determine habitat degradation level (high, medium, and low). Three values were calculated for habitat degradation at each site based on the aggregated characteristics of soil, vegetation, and the 2 data sets combined. We selected only those sites classified as having high- or low-degradation levels for these analyses.

Because of the discontinuous nature of the habitats being sampled with various types of vegetation interspersed along the length of these canyons, transects varied from 120 to 200 m long and 8 to 40 m wide depending upon available habitat. High elevations and late snowmelt generally delayed onset of breeding at these sites; hence, transects to census breeding birds were walked once each year during a 10-d block in 1994 (26 June–5 July) and 1995 (27 June–6 July). Sites were visited between 05:30 and 09:30 h by 2 people, an observer and a recorder, walking at a constant pace (maximum 10 m per min). Start and finish times were recorded so that data from transects of different lengths could be standardized. All songbirds seen or heard were recorded as occurring within the specified riparian area or in the adjacent sagebrush (*Artemisia* spp.) or pinyon pine–juniper (*Pinus monophyla–Juniperus* spp.) habitat. Only those individuals within the riparian habitat, or actively foraging in the air above the riparian area (e.g., Violet-green Swallows, *Tachycineta thalassina*), were included in this analysis.

We analyzed species richness and species richness values standardized to account for the amount of time spent on each transect. Although correcting time-standardized species richness values for unequal sampling effort may be required under some circumstances (Elphick 1997a), examination of residual values for the linear model of species richness = time revealed a normal distribution for our data. In addition, we calculated species diversity for each transect. Because of the potential for differential attraction to riparian habitats among the species examined, we followed Magurran (1988) and used Brillouin's index (1962):

$$\mathrm{HB} = \frac{\ln N! - \sum \ln n_i!}{N}$$

For statistical analyses, each of these 3 measurements (species richness, time-standardized species richness, and species diversity) formed the dependent continuous variable in a general linear model (PROC GLM; SAS Institute Inc. 1988), with the independent categorical variables being degradation level (based on aggregate characteristics of soil, vegetation, or the 2 combined), habitat type, year, and all possible interaction terms for the 3 variables. Because each possible response variable gave the same qualitative pattern of results for each degradation measure, we report only those values for species richness and the combined degradation measure. Brillouin's index takes into account both evenness and species richness in a composite measure; therefore, we also assessed species overlap within and between sites of the 2 degradation levels for each habitat type by calculating Sorenson's index (Southwood 1978):

$$C_s = \frac{2j}{(a + b)}$$

In addition, we examined the rarity of those species encountered on the basis of Gaston's (1994) definition, which uses the arbitrary cutoff of the least common 25% of bird species.

To examine how individual species reacted to degradation level in the 4 habitat types, we conducted analyses similar to that above but substituted abundance in place of species richness for each of the 6 most common species observed (American Robin, *Turdus migratorius*; House Wren, *Troglodytes aedon*; Red-naped Sapsucker, *Sphyrapicus nuchalis*; Warbling Vireo, *Vireo gilvus*; Yellow Warbler, *Dendroica petechia*; and Brewer's Blackbird, *Euphagus cyanocephalus*).

Meadow Watches

Preliminary censuses indicated that meadows had substantially lower species richness when compared with the other 3 habitats. To ensure that this was an accurate reflection of circumstances, we expanded our examination of meadow habitat. Ten moist meadow sites adjacent to sagebrush or pinyon pine–juniper habitat (the 9 mentioned above plus 1 additional site) were selected for observation of avian activity in a 30 × 20-m section of each meadow, which typically was the entire meadow. Meadow use was assessed at each site during a 10-d period in the breeding season (26 June–5 July 1994 and 27 June–6 July 1995), and repeated during a 10-d period in the premigratory season (29 July–7 August 1994 and 25 July–3 August 1995) to test for seasonal change in meadow use. For both seasons, one 30-min sample was collected for each meadow by 2 observers during a 3-h period (06:00–09:00 h). Although birds were not individually marked, observers attempted to monitor movements in and out of the meadow to avoid counting the same individual more than once. Therefore, our data reflect only a minimum estimate of species diversity. Birds flying over the meadow were not included in the data, with the exception of swallows searching for prey. Meadow watch data were converted to indices of species diversity based on Brillouin's measure (1962). These data then were used as the basis for subsequent analyses to test for differences in species diversity at meadow sites between and within years using Wilcoxon's matched-pairs test (Zar 1996:167).

RESULTS

General Censuses

Analysis of species richness indicated a significant interaction effect between habitat type and degradation level (Table 1). Examining these data graphically (Fig. 1) revealed that among minimally degraded (i.e., high-quality) sites, there were similar levels of species richness for all 4 habitat types. Comparing highly degraded sites for each habitat, however, revealed that avian species richness values were lower in meadows and higher in aspen-, willow-, and birch-dominated habitats (although not statistically significantly so; Table 1) than values obtained for minimally degraded sites. The latter result suggested that observed levels of degradation of forested riparian habitats created opportunities for new species, normally not found in minimally degraded habitats, to move into aspen-, willow-, and birch-dominated stands.

Across habitat types, species overlap values in low-degradation sites were greater in birch than any other habitat type (Table 2). Within habitat type, however, the amount of overlap was greater in low-degradation than high-degradation sites, with the exception of aspen where the trend was reversed. Other than meadows, values of overlap between low- and high-degradation sites were intermediate to those of within-degradation level values. Some caution must be used when interpreting these species overlap data due to the generally low number of species encountered at many sites during the study (see average values reported in Fig. 1).

At a species-specific level, we identified 6 species that were encountered at ≥2 sites in highly, but not minimally, degraded forested habitats during our transects. These species may act as indicators of habitat degradation in riparian forested areas of the Toiyabe Mountain Range: Downy Woodpecker (*Picoides pubescens*) and Lazuli Bunting (*Passerina amoena*) occurred in highly degraded birch and willow, Plumbeous Vireo (*Vireo plumbeus*) in highly degraded willow and aspen, and Green-tailed Towhee (*Pipilo chlorurus*), Dark-eyed Junco (*Junco hyemalis*), and Pine Siskin (*Carduelis pinus*) in highly degraded aspen.

When we examined changes in abundance of the 6 most common species observed during the study, we detected no degradation effect, but habitat was a useful predictor of species abundance for 4 of 6 species. Aspen was used more often than other habitats by House Wrens (Habitat: $F_{3,68} = 22.71$, $P = 0.0001$), Red-naped Sapsuckers (Habitat: $F_{3,68} = 4.61$, $P = 0.0092$), and Warbling Vireos (Habitat: $F_{3,68} = 10.67$, $P = 0.0001$); individuals of the latter species also frequently were

TABLE 1. Analysis of variance test of the effects of degradation, habitat, and year on species richness of riparian birds for 4 habitat types in the Toiyabe Mountain Range, Nevada.

Source[a]	SS[b]	df	F	P
Degradation	0.05	1	0.00	0.949
Habitat	190.88	3	5.55	0.002
Year	8.41	1	0.73	0.395
Degradation × Habitat	108.06	3	3.14	0.031
Degradation × Year	6.46	1	0.56	0.455
Habitat × Year	31.39	3	0.91	0.439
Degradation × Habitat × Year	43.55	3	1.27	0.292
Error	779.39	68		

[a] Model $F_{15,68} = 2.73$, $P = 0.0025$

[b] Type III sums of squares

TABLE 2. Comparison of Sorensen's index values (mean ± $s_{\bar{x}}$, n) for riparian birds at 42 sites representing high- and low-degradation levels for 4 habitat types in the Toiyabe Mountain Range, Nevada.

	Birch	Willow	Aspen	Meadow
Low degradation	0.459 ± 0.078 (3)	0.362 ± 0.032 (15)	0.229 ± 0.019 (3)	0.150 ± 0.080 (6)
High degradation	0.175 ± 0.057 (10)	0.249 ± 0.033 (36)	0.554 ± 0.031 (21)	0.050 ± 0.050 (10)
High v. Low	0.194 ± 0.040 (15)	0.301 ± 0.023 (54)	0.394 ± 0.033 (21)	0.031 ± 0.022 (20)

encountered in birch, while Brewer's Blackbirds rarely were observed outside of meadows (Habitat: $F_{3,68} = 2.91$, $P = 0.0405$). The interaction of habitat type and degradation level was significant for both American Robins (Degradation × Habitat: $F_{3,68} = 5.63$, $P = 0.0023$) and Yellow Warblers (Degradation × Habitat: $F_{3,68} = 3.45$, $P = 0.0213$). Each of these 2 species was found more often in highly degraded birch and either intact willows (American Robins) or intact meadows (Yellow Warblers).

Based on Gaston's (1994) definition of rarity, among the individuals encountered during these censuses, 12 species comprised 75% of all individuals sighted, and 32 species could be classified as rare. However, previous work by one of us (Reed 1996) suggests that there can be substantial difficulties in ascertaining the actual absence of rare species from a census site. As a consequence, rare species probably make the poorest indicators of habitat impact, and we will not address the issue of rarity any further.

Meadow Watches

Species diversity indices from meadow watches varied seasonally and annually (Table 3), with substantial differences in number of individuals and species encountered. No significant difference in species diversity was found in meadow sites during breeding seasons of 1994 and 1995 (Wilcoxon's matched pairs test: $Z = 0.0$, $n = 10$, $P = 1.0$). However, activity (as reflected in diversity measures) in these meadows increased sharply during the post-breeding, pre-migratory period of the dry

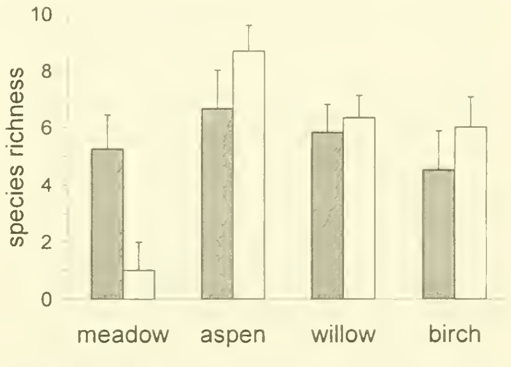

Fig. 1. Mean bird species richness (± $s_{\bar{x}}$) for 4 riparian habitats in the Toiyabe Mountain Range, Nevada. Shaded bars represent values for minimally degraded sites; open bars represent highly degraded sites.

TABLE 3. Comparison of Brillouin's species diversity index values (mean ± $s_{\bar{x}}$) for riparian birds at 10 meadow sites in the Toiyabe Mountains of central Nevada.

Year	Season	Diversity
1994	Breeding	0.062 ± 0.042
	Pre-migratory	0.254 ± 0.080
1995	Breeding	0.056 ± 0.030
	Pre-migratory	0.088 ± 0.054

year (1994; $Z = 2.201$, $n = 10$, $P = 0.0277$), while it rose marginally but not significantly in the wet year (1995; $Z = 0.534$, $n = 10$, $P = 0.5929$).

DISCUSSION

Previous studies (primarily focusing on grazing) show no single effect of change in habitat condition on riparian bird communities; even studies of the same bird species in different locations differ in their conclusions regarding the impact of change in habitat condition (Saab et al. 1995 and citations therein). In part, this ambiguity comes from comparing studies from different habitat types and with different levels of habitat degradation. We controlled for both factors *a priori* in our study area and found that habitat degradation did affect avifaunal communities, but its impact differed among habitats examined. While bird communities in meadows were strongly and adversely affected by increased degradation, species richness in forested riparian habitats was consistently higher on degraded sites. We note, however, that while lowered species richness on high-quality areas would be an adverse impact, increased richness or diversity on degraded sites does not necessarily equate with "better" habitat when assessing conservation requirements. This greater species richness in highly degraded forest habitat may reflect the creation of additional opportunities in these habitats for "new" species such as Lazuli Buntings and Pine Siskins, which normally were not found in minimally degraded areas. That is, species that use degraded habitats were added to the community while few associated with undegraded habitats were lost. But an increase in species richness with increased habitat degradation is not necessarily monotonic. Birds will disappear from forests in which the structure has been too drastically altered to continue meeting their habitat requirements, whereas intermediate levels of disturbance may increase species richness in a variety of habitats (Connell 1978).

Within meadow habitat, degradation had strong adverse effects on bird communities, likely due to the susceptibility of meadow vegetation and stream bank morphology to cattle grazing (see introductory paragraphs for references). However, we also identified for meadows a seasonal effect on species diversity that was of a larger magnitude in the dry year (1994) than the wet year (1995). The significantly higher species diversity found during the pre-migratory period of 1994 suggests that birds are constrained more in their choices of habitat during dry than wet years by lack of moist meadows and other water sources. We presume that availability of suitable foraging or resting locations along water courses differs between years, being more restricted in drier years. During dry years, especially late in the season, low-lying wet meadows (such as those studied here) may be the only places where water is available.

Bock et al.'s (1993) review of literature on the impact of grazing on birds suggested that American Robins, Brewer's Blackbirds, and House Wrens would be positively affected by grazing (i.e., have increased population densities), while studies of Red-naped Sapsuckers, Warbling Vireos, and Yellow Warblers provided only mixed or uncertain results. In our analyses there was no significant impact of habitat degradation on numbers encountered for 4 of 6 species. Interaction effects that we uncovered indicate that degradation's impact differs among habitat types but, in this study, led to increased numbers of both American Robins and Yellow Warblers in certain habitats.

Sedgwick and Knopf (1991) expressed concern about the short duration of most studies on grazing impacts in terms of how long-term grazing may alter the plant community. We share this concern about study duration, but from the standpoint of missing the years in which impacts are most noticeable. We had 2 very different years in our sample. Our overall results suggest that single-year studies can provide misleading results when examining impacts of habitat degradation. Years during which conditions are the most extreme may be the most useful in identifying critical habitat.

Also, the importance of certain sites (here, meadows) can be overlooked if surveyed during the wrong season (breeding season versus pre-migratory period).

The majority of studies on potential impacts of grazing (or some other factor affecting habitat condition) have no replication and often lack controls. Resource managers need to use appropriate experimental designs when testing hypotheses such as those assessing potential impacts of grazing (Romesburg 1981, MacNab 1983, Gavin 1989, Murphy and Noon 1991). However, large-scale experimental studies are uncommon, in part because of limited resources and in part due to logistical inconvenience of such studies. With appropriate planning, experimental approaches often are possible (cf. Elphick 1997b). In our study we had 4 habitat treatments and 2 levels of degradation, with replication for each treatment combination. If we had been able to assign which plots received each level of degradation, rather than using already treated areas, such assignments would have increased the strength of our study. However, our experimental design is a good example of using space for time, and we recommend it for conservation-related studies that do not have time as a resource.

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BAT DISTRIBUTION AND HIBERNACULA USE IN WEST CENTRAL NEVADA

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ABSTRACT.—We captured 299 individuals of 11 bat species in mist-nets at 18 water sources in west central Nevada from June through August 1994. *Myotis ciliolabrum*, *Pipistrellus hesperus*, *M. californicus*, and *Corynorhinus townsendii* were the most common species captured. These species are apparently broadly distributed throughout west central Nevada, occurring in a variety of habitat types. We captured *Euderma maculatum* at 2 localities. These represent the 1st known records of this species in Esmeralda County, Nevada. Mine adits were surveyed for hibernating bats from December 1994 through February 1995. We determined the presence of 3 hibernating species: *C. townsendii*, *M. ciliolabrum*, and *P. hesperus*. Bats were present in 19 of 70 mines (27%) we surveyed at elevations ranging from 1500 m to 2460 m. *C. townsendii* was the most common species encountered. Our study provides some much-needed baseline data on bat distribution and use of mines for hibernacula in west central Nevada.

Key words: Chiroptera, bats, Nevada, distribution, Great Basin, Euderma maculatum.

Over the past few decades, the effects of habitat loss, and both destruction and disturbance at roost sites, have negatively affected some bat populations (Humphrey 1978, Tuttle 1979, Richter et al. 1993). Concern over declining populations and the subsequent federal listing of some species have increased both public and natural resource agency interest in bat conservation. Unfortunately, data necessary to develop meaningful conservation and management plans for bat species are often lacking. Even such basic information as species distribution is not available for many locations (Saugey 1991), including much of the state of Nevada. The distribution of bats within the state was first summarized by Hall (1946). Recently, Ports and Bradley (1996) provided new information on distribution and habitat affinities of bats in eastern and northeastern parts of the state. Current information on bat distribution in other parts of Nevada is still lacking. Our study was initiated to gather data on the distribution of bat species found in the west central part of the state.

STUDY AREA

Our study was conducted in Esmeralda County, southwestern Mineral County, and a small portion of southwestern Nye County, Nevada (Fig. 1). The study region includes several broad alluvial valleys and flats separated by 7 large mountain ranges and many isolated peaks. Elevation ranges from 1200 m to >2800 m. Mean annual precipitation ranges from 10 cm to 40 cm (Houghton et al. 1975). Vegetation in this region is characteristic of the Great Basin, dominated by sagebrush (*Artemisia* spp.) or saltbush (*Atriplex* spp.) associations at low elevations and pinyon pine (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) at higher elevations (Turner 1982).

To examine patterns of distribution by different bat species, we classified each survey site into 3 habitat types: water sources surrounded by desert shrubs such as sagebrush (*Artemisia* spp.) or saltbush (*Atriplex* spp.), elevation approximately 1200–2000 m; water sources surrounded by pinyon pine and juniper, elevation approximately 2000–2900 m; and streams lined with deciduous trees such as cottonwood (*Populus* spp.), willow (*Salix* spp.), or quaking aspen (*Populus tremuloides*), elevation approximately 2150–2800 m. We used categories similar to those of Ports and Bradley (1996) to aid in comparisons between their study and ours.

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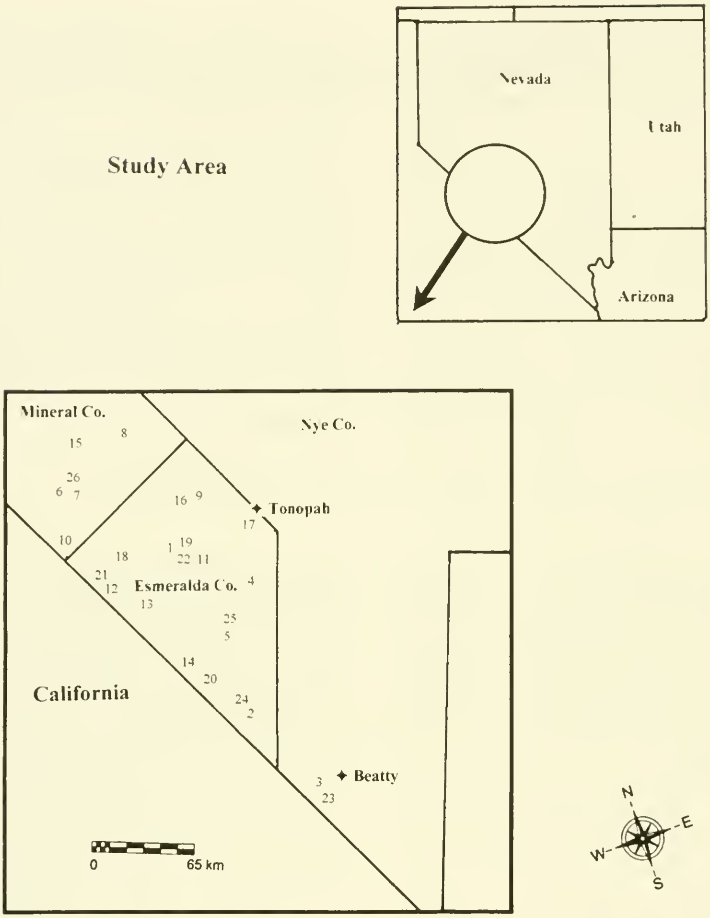

Fig. 1. Location of sites in west central Nevada in which bat surveys were conducted, June 1994 through February 1995.

METHODS

Mist-netting Surveys

We captured bats using 2 × 12-m, 36-mm mesh, 50-denier mist-nets placed across or along edges of perennial streams, ponds, springs, and troughs from June through August 1994. Nets were opened at dusk and left open for 3–4 h depending upon bat activity, which normally decreased rapidly 3 h after dusk. Captured bats were identified to species and sexed. The reproductive condition of females was assessed by visual examination of the lower abdomen and mammary glands (Racey 1988). All captured bats were released after handling.

Myotis californicus and *M. ciliolabrum* are difficult to distinguish from one another in some localities. In west central Nevada we used a combination of characteristics including pelage coloration (Barbour and Davis 1969, Hall 1981, Szewczak et al. 1998), pattern of hair covering the snout (van Zyll de Jong 1985), forehead profile, and length of the 3rd metacarpal (Bogan 1974) to differentiate between the 2 species.

Echolocation calls of *Euderma maculatum* are audible to the human ear, allowing species recognition without direct capture (Leonard and Fenton 1984). At some of our survey sites the presence of this species was determined from echolocation calls rather than mist-net captures.

Mine Surveys

Mine surveys were conducted from mid-December 1994 through February 1995. Single entries were made into mines to locate

TABLE 1. Number of bats captured by species from west central Nevada, June–August 1994.

	Number captured	Percent of total captures	Percent of sites
Myotis californicus	46	15.4	61.1
Myotis ciliolabrum	84	28.1	66.7
Myotis evotis	19	6.4	16.6
Myotis volans	5	1.6	0.6
Lasionycteris noctivagans	6	2.0	0.6
Eptesicus fuscus	15	5.0	0.6
Pipistrellus hesperus	80	26.8	44.4
Corynorhinus townsendii	24	8.0	44.4
Euderma maculatum	3	1.0	27.8[a]
Antrozous pallidus	15	5.0	33.3
Tadarida brasiliensis	2	0.7	0.6
TOTAL	299	100.0	

[a]Includes 2 sites where *E. maculatum* presence was determined from echolocation calls.

TABLE 2. Occurrence of bat species by locality (see Appendix) and habitat type (S = water sources surrounded by desert shrubs, P = higher-elevation water sources surrounded by pinyon-juniper, D = streams lined by deciduous trees) for each species in west central Nevada, June–August 1994.

	Localities (Appendix)	Habitat type
Myotis californicus	2, 3, 6, 7, 9, 10, 12, 14–17	S, P, D
Myotis ciliolabrum	1, 2, 4, 6–12, 14, 15	S, P, D
Myotis evotis	8, 10, 15	P, D
Myotis volans	14	P
Lasionycteris noctivagans	15	P
Eptesicus fuscus	14	P
Pipistrellus hesperus	3, 6, 7, 9, 11, 14, 16, 17	S, P
Corynorhinus townsendii	2, 4, 5, 7, 8, 14, 15, 17	S, P
Euderma maculatum	4, 8, 11, 14, 18	S, P
Antrozous pallidus	6, 7, 8, 13, 14, 15	S, P
Tadarida brasiliensis	11	S

hibernating bats. We chose areas to be surveyed by consulting USGS 7.5′ topographical maps. Mine adits that appeared unsafe or that were actively being mined were not surveyed. Mines were deemed unsafe if we questioned the stability of walls and/or ceilings. All shafts were considered hazardous and thus not entered. We measured temperature and relative humidity at the entrance of each mine and at 10-m intervals throughout the adit using a digital hygrometer (Protimeter, Bucks, England).

Mines were explored and all accessible reaches inspected for hibernating bats. We took care to minimize disturbance to bats by moving quietly and quickly through the mine. We determined species present by non-contact visual inspection. Temperature and relative humidity were measured at each roost site. Average temperature and relative humidity in mines that contained bats and those that did not were compared using a 2-tailed t test (Zar 1984).

RESULTS

Mist-netting Surveys

We identified a total of 299 individuals of 11 species from 18 water sources in 21 trapnights from west central Nevada (Table 1). *M. californicus* and *M. ciliolabrum* were the most broadly distributed species within the study region (Table 2). *M. ciliolabrum* occurred in all habitat types and was the most abundant species captured in west central Nevada. *M. californicus* occurred in all habitat types and was the 3rd most abundant species captured. Two other species of *Myotis* (*M. volans* and *M. evotis*) were less common. *M. volans* was captured at only 1 site in mid-elevation pinyon-juniper woodlands. *M. evotis* occurred in pinyon-juniper woodlands and in riparian stream corridors.

Pipistrellus hesperus was the 2nd most abundant species captured in west central Nevada. *P. hesperus* was captured at 44% of the survey sites, occurring in both desert shrub and pinyon-juniper woodlands. *Corynorhinus townsendii*, captured at over half the water sources surveyed, occurred in desert shrub and pinyon-juniper woodlands.

E. maculatum was captured at 2 sites in Esmeralda County (Table 1, Appendix). Echolocation calls were used to determine this species' presence at 2 additional sites in Esmeralda County and 1 site in Mineral County. *E. maculatum* occurred in both desert shrub areas and pinyon-juniper woodlands. *Antrozous pallidus* was also found in these 2 habitats and was captured at 4 of 18 sites.

Lasionycteris noctivagans, *Eptesicus fuscus*, and *Tadarida brasiliensis* were detected at only 1 site each in west central Nevada. Both *L. noctivagans* and *E. fuscus* were captured only in pinyon-juniper woodlands, while *T. brasiliensis* was captured only in low-elevation desert shrub.

Reproductive females (pregnant, lactating, post-lactating) were captured in 9 of 11 species

TABLE 3. Reproductive status of female bats captured in west central Nevada, June–August 1994.

Bat species	Total captured	Number pregnant	Number lactating	Number post-lactating	Percent reproductive
Myotis ciliolabrum	51	9	3	9	41.2
Myotis californicus	29	0	3	9	41.4
Myotis evotis	8	0	1	1	25.0
Myotis volans	4	0	0	0	0.0
Lasionycteris noctivagans	4	0	0	1	25.0
Eptesicus fuscus	7	0	3	0	42.9
Pipistrellus hesperus	59	28	10	1	66.1
Corynorhinus townsendii	14	3	2	4	64.3
Euderma maculatum	1	0	0	0	0.0
Antrozous pallidus	8	2	4	1	87.5
Tadarida brasiliensis	2	1	0	0	50.0

present in west central Nevada (Table 3). Over half of all females captured were reproductive at capture. The percentage of females reproductively active for any 1 species ranged from 0% for *M. volans* and *E. maculatum* to 87.5% for *A. pallidus*. Pregnant females of *A. pallidus*, *M. ciliolabrum*, *M. californicus*, *C. townsendii*, and *P. hesperus* were captured until the 1st week in July (Appendix). We began capturing lactating females around this same time.

Mine Surveys

We determined the presence of 3 hibernating species: *C. townsendii*, *M. ciliolabrum*, and *P. hesperus* in west central Nevada. Nineteen of 70 mines we surveyed contained a total of 42 *C. townsendii*, 12 *M. ciliolabrum*, and 4 *P. hesperus* (Table 4). These mines were located at elevations ranging from 1500 m to 2460 m (Appendix). *C. townsendii* was the most common species encountered, present in 16 of 19 mines that contained bats (Table 4). *M. ciliolabrum* was found in 7 of 19 mines (37%) and *P. hesperus* in 3 of 19 (16%). Six mines contained more than 1 species of hibernating bat, hibernating as near as 0.5 m to one another. Most mines (68%), however, contained only 1 species. Individuals of the 3 species were always observed hibernating singly; we never observed clusters of bats in any of the mines surveyed.

We found no difference in average temperature between mines that contained bats and those that did not ($t = 0.81$, 68 df, $P = 0.42$) and no difference in average relative humidity ($t = 0.11$, 68 df, $P = 0.91$). The average temperature in mines containing bats ranged from 0.4°C to 18.6°C (Table 4). Relative humidity in these mines ranged from 22% to 58%. In most instances bats selected roosts with cooler temperatures and higher humidities than the average for that mine (Table 4). *C. townsendii* was found hibernating at locations with air temperatures of 0.0–17.0°C ($\bar{x} = 6.1 \pm 4.9$) and relative humidity of 21.0–66.0% ($\bar{x} = 41.8 \pm 12.6$). *M. ciliolabrum* occurred at air temperatures of 1.0–17.0°C ($\bar{x} = 5.2 \pm 4.3$) and relative humidity of 24.0–66.0% ($\bar{x} = 48.5 \pm 10.2$), while *P. hesperus* hibernacula had air temperatures from 0.0°C to 14.0°C ($\bar{x} = 7.3 \pm 5.7$) and relative humidity of 21.0–52.0% ($\bar{x} = 37.3 \pm 12.7$).

DISCUSSION

Hall (1946) provided maps of the probable distribution of bat species in Nevada. However, specimens and other records of occurrence within these distributions were limited to relatively few locations. Our results contribute some new locality records for bat species in west central Nevada.

Of special interest during our study was the capture and audible detection of *E. maculatum*. This species is distributed throughout western North America (Watkins 1977, Hall 1981) and occurs in vegetation zones ranging from desert shrub to montane coniferous forest (Handley 1959, Findley and Jones 1965). Although *E. maculatum* may be locally abundant (Woodsworth et al. 1981, Leonard and Fenton 1983, 1984), it is considered rare over its geographic range (Watkins 1977). In Nevada *E. maculatum* is known from only 5 localities (Best 1988). The 2 sites in which we captured *E. maculatum* represent the 1st known records of this species in Esmeralda County. In addition, there are no records of *E. maculatum* in Mineral County, where we detected its presence based on echolocation calls.

TABLE 4. Mean temperature and relative humidity (± standard deviation) of mine tunnels in west central Nevada that contained bats during winter 1995, and number of each species observed with mean temperature and mean relative humidity at their roosting sites within those mines.

Location[a]	Temperature (C°)	Relative humidity (%)	*Corynorhinus townsendii*	*Myotis ciliolabrum*	*Pipistrellus hesperus*
			No. (temperature, relative humidity)		
19 (a)	4.8 ± 1.7	42.3 ± 3.1	1 (3.0, 48.0)	0	0
19 (b)	0.4 ± 1.0	47.8 ± 3.5	2 (0.5, 46.5)	0	1 (0.0, 46.0)
19 (c)	0.9 ± 1.1	49.0 ± 2.3	1 (0.0, 52.0)	0	0
19 (d)	2.3 ± 1.3	45.8 ± 0.5	1 (3.0, 47.0)	0	0
20	14.5 ± 0.7	34.3 ± 4.9	0	1 (17.0, 24.0)	0
21 (a)	2.3 ± 1.1	43.3 ± 2.7	4 (1.0, 41.5)	0	0
21 (b)	6.1 ± 1.9	35.4 ± 6.1	0	1 (8.0, 53.0)	0
21 (c)	5.4 ± 1.9	41.3 ± 3.1	1 (5.0, 47.0)	2 (4.5, 46.0)	0
21 (d)	7.0 ± 2.1	36.7 ± 3.4	2 (6.0, 38.0)	0	0
22 (a)	2.7 ± 0.5	46.2 ± 1.3	1 (3.0, 49.0)	0	0
22 (b)	5.0 ± 2.1	44.5 ± 7.2	1 (4.0, 45.0)	2 (6.0, 42.5)	0
23	18.6 ± 1.7	28.1 ± 5.5	2 (17.0, 32.0)	0	0
24 (a)	12.7 ± 3.1	22.3 ± 2.5	8 (12.3, 22.3)	0	1 (14.0, 21.0)
24 (b)	9.5 ± 1.0	42.5 ± 7.8	2 (9.0, 41.0)	0	0
25	9.6 ± 2.1	39.3 ± 13.2	7 (7.7, 37.7)	0	2 (7.5, 38.0)
26 (a)	8.1 ± 3.8	46.3 ± 6.3	1 (4.0, 51.0)	3 (3.7, 50.1)	0
26 (b)	2.0 ± 1.8	57.8 ± 5.5	7 (1.1, 60.7)	2 (2.0, 61.0)	0
26 (c)	5.6 ± 4.7	47.9 ± 7.8	0	1 (1.0, 55.0)	0
26 (d)	13.1 ± 4.7	34.7 ± 10.0	1 (7.0, 49.0)	0	0

[a]See Appendix

Another species for which there is no previous record of occurrence in Mineral County is *A. pallidus* (Hall 1946). We captured reproductive females at 4 locations within this county. Although locality records exist for northern Mineral County, our captures of *M. ciliolabrum*, *M. californicus*, *M. evotis*, *P. hesperus*, and *L. noctivagans* are all new records for the southern part of the county.

We determined the presence of 11 species of bats in west central Nevada. *M. ciliolabrum*, *P. hesperus*, *M. californicus*, and *C. townsendii* were the most common species captured. These species are apparently broadly distributed in this portion of Nevada, occurring in a variety of habitat types. Ports and Bradley (1996) found *M. ciliolabrum* and *C. townsendii* to be widely distributed in a variety of habitats throughout eastern Nevada; *P. hesperus* was rare in eastern Nevada, and *M. californicus* did not occur. In the White/Inyo Mountains of eastern California and western Nevada, both *P. hesperus* and *M. californicus* are relatively common and occur in many different vegetation zones (Szewczak et al. 1998).

L. noctivagans was one of the rarest species we found, being captured at only 1 site. Hall (1946) reported only 2 locality records for this species within our study region, both from Esmeralda County. Ports and Bradley (1996) found this species to occur only in high-elevation areas that had a combination of coniferous and/or deciduous trees. Male and nonreproductive female *L. noctivagans* roost alone under loose bark or in crevices in dead or dying trees (Campbell et al. 1996, Mattson et al. 1996), while reproductively active females form maternity colonies in tree cavities (Campbell et al. 1996, Betts 1998). It is possible that suitable roost sites for this species are limited in west central Nevada. However, given the large scale at which we conducted our surveys, we made no attempt to quantify the availability of potential roost sites.

E. fuscus also was captured at only 1 location. Szewczak et al. (1998) captured this species only upstream from ranches with established agricultural fields. *E. fuscus* is commonly associated with buildings (Barbour and Davis 1869), which are rare in the areas we surveyed. This lack of man-made structures may be a factor in the limited distribution of *E. fuscus* within our study region. However, *E. fuscus* is also known to roost in trees and rock crevices (Kurta and Baker 1990).

Over half of all female bats we captured were reproductively active. Although limited, our sample sizes do provide some indication of dates of parturition. Based on our capture data, *A. pallidus*, *M. ciliolabrum*, *M. californicus*, *C. townsendii*, and *P. hesperus* in west central Nevada likely give birth sometime in late June or early July. These dates are similar to those reported by Hall (1946).

The number of individuals and species we captured at individual sites was highly variable. Our mist-netting surveys focused on water sources. Preference for foraging over open water varies with bat species (Fenton et al. 1980), and interspecific foraging strategies may have influenced the species captured. However, during active periods most bat species do drink nightly (Kunz 1982), and many of the water sources we visited were the only ones available for many kilometers in any direction. It is likely that bat populations in these areas are dependent on these isolated water supplies. Other factors that possibly influenced our capture results are the placement and configuration of mist-nets (Kunz and Kurta 1988) and temporal variation in bat activity (Hayes 1997).

C. townsendii, M. ciliolabrum, and *P. hesperus* were found hibernating in 27% of the mines we surveyed. Similar results have been obtained by others. In a winter survey of 85 mines in central Nevada, Alcorn (1944) found 14 *C. townsendii* in 12 mines, 19 *M. ciliolabrum* in 14 mines, and 6 *P. hesperus* in 3 mines. Szewczak et al. (1998) also found *C. townsendii* and *M. ciliolabrum* to be scattered sparsely throughout mines in the Inyo and White Mountains of eastern California and western Nevada.

We found no difference in average temperature and relative humidity between used and nonused mines. However, evidence suggests that bats select hibernacula that provide stable temperature and humidity regimes (Humphrey 1978, Genter 1986). Since our temperature and relative humidity data were collected on only a single visit, we have no information on how these varied over the winter. A lack of mines providing stable environments would help explain why the majority of mines we surveyed did not contain bats.

Thorough knowledge of the current distribution of any species is necessary to maintain existing populations. Results of this study contribute some important information on bat distribution and use of mine adits for hibernacula in west central Nevada, but much work remains to be done. Data on roost and foraging-site selection are needed to develop a better understanding of bat species within this region.

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APPENDIX. Locations of survey sites and species examined from west central Nevada, 1994–1995.

1. Cave Springs (S)[a], Silver Peak Range, Esmeralda Co., Nevada. E425700, N4174100[b], 1860 m. 1 June 1994. *M. ciliolabrum* (2 males).
2. Old Camp (P), Gold Mountain, Esmeralda Co., Nevada. E471200, N4123300, 2085 m. 16 June 1994. *M. californicus* (2 males, 2 nonreproductive females), *M. ciliolabrum* (1 male, 2 nonreproductive females), *C. townsendii* (1 male).
3. Lower Indian Springs (S), Bullfrog Hills, Nye Co., Nevada. E518100, N4088500, 1220 m. 19 June 1994. *M. californicus* (1 nonreproductive female), *P. hesperus* (1 male, 2 pregnant females).
4. Dago Joe Springs (P), Montezuma Range, Esmeralda Co., Nevada. E471600, N4174600, 2060 m. 22 June 1994. *M. ciliolabrum* (17 males, 6 pregnant females), *C. townsendii* (2 males, 2 pregnant females), *E. maculatum* (1 male).
5. Unnamed spring, 0.2 km east of Blue Dick Mine (P), Palmetto Mountains, Esmeralda Co., Nevada. E413500, N4145600, 2185 m. 24 June 1994. *C. townsendii* (2 nonreproductive females).
6. Unnamed spring, 4 km south of Teel's Marsh and 0.5 km northeast of Rock House Springs (S), Mineral Co., Nevada. E380600, N4223200, 1600 m. 6 July 1994. *M. californicus* (1 nonreproductive female), *M. ciliolabrum* (1 male, 11 nonreproductive females), *P. hesperus* (7 males, 1 pregnant female, 6 lactating females, 8 nonreproductive females), *A. pallidus* (1 pregnant female).
7. Company Springs, 4.25 km south of Teel's Marsh (S), Mineral Co., Nevada. E380200, N4223400, 1540 m. 7 July 1994. *M. californicus* (4 nonreproductive females), *M. ciliolabrum* (3 males, 3 pregnant females, 1 lactating female, 12 nonreproductive females), *P. hesperus* (2 males, 24 pregnant females, 2 nonreproductive females), *C. townsendii* (1 nonreproductive female, 1 pregnant female), *A. pallidus* (1 pregnant female).
8. Dunlap Tunnel Springs (P), Pilot Mountains, Mineral Co., Nevada. E415700, N4244900, 2330 m. 9 July 1994. *M. ciliolabrum* (1 male, 2 lactating females, 2 nonreproductive females), *M. evotis* (3 males, 1 lactating female, 1 nonreproductive female), *C. townsendii* (3 males, 1 lactating female), *E. maculatum* (audible detection), *A. pallidus* (1 lactating female).
9. Crow Springs (S), Monte Cristo Range, Esmeralda Co., Nevada. E448300, N4233400, 1575 m. 11 July 1994. *M. californicus* (1 male, 1 lactating female, 3 nonreproductive females), *M. ciliolabrum* (2 males, 2 post-lactating females, 1 nonreproductive female), *P. hesperus* (3 males, 1 lactating female, 1 unknown escapee).

10. Pinchot Creek (D), White Mountains, Esmeralda Co., Nevada. E387600, N4198100, 2360 m. 13 July 1994. *M. californicus* (1 nonreproductive female), *M. ciliolabrum* (1 male, 2 nonreproductive females), *M. evotis* (1 male).
11. Cottonwood Springs (S), Silver Peak Range, Esmeralda Co., Nevada. E431500, N4174100, 1920 m. 19 July 1994. *M. ciliolabrum* (1 male), *P. hesperus* (2 males), *E. maculatum* (audible detection), *T. brasiliensis* (1 nonreproductive female, 1 lactating female).
12. Middle Creek (D), White Mountains, Esmeralda Co., Nevada. E391400, N4188800, 2155 m. 20 July 1994. *M. californicus* (1 lactating female, 1 nonreproductive female), *M. ciliolabrum* (1 nonreproductive female).
13. Dyer Reservoir (S), Dyer, Esmeralda Co., Nevada. E404600, N4170500, 1465 m. 24 July 1994. *A. pallidus* (1 lactating female).
14. Pigeon Springs (P), Sylvania Mountains, Esmeralda Co., Nevada. E441000, N4141000, 2000 m. 25 July 1994. *M. californicus* (3 males, 1 nonreproductive female), *E. fuscus* (4 males, 3 lactating females, 2 nonreproductive females), *P. hesperus* (2 lactating females, 2 nonlactating females), *C. townsendii* (1 nonreproductive female), *E. maculatum* (1 nonreproductive female), *A. pallidus* (5 males, 2 lactating females). 2 August 1994. *M. californicus* (1 male), *M. ciliolabrum* (2 males, 1 female), *M. volans* (1 males, 4 females), *E. fuscus* (4 males, 2 females), *P. hesperus* (4 males, 6 females), *E. maculatum* (1 male), *A. pallidus* (2 males, 1 female).
15. Pepper Springs (P), Excelsior Mountains, Mineral Co., Nevada. E391000, N4242500, 2010 m. 3 August 1994. *M. californicus* (2 males, 1 post-lactating female), *M. ciliolabrum* (1 male, 3 nonreproductive females, 3 post-lactating females), *M. evotis* (7 males, 5 nonreproductive females 1 post-lactating female), *L. noctivagans* (2 males, 1 post-lactating female, 3 nonreproductive females), *C. townsendii* (3 males, 1 lactating female, 2 post-lactating females, 1 nonreproductive female), *A. pallidus* (1 post-lactating female).
16. Cook Springs (S), Monte Cristo Range, Esmeralda Co., Nevada. E448400, N4233400, 1920 m. 5 August 1994. *M. californicus* (6 males, 1 lactating female, 7 post-lactating females, 1 nonreproductive female, 1 unknown escapee), *P. hesperus* (1 male, 1 nonreproductive female).
17. Willow Springs (S), Weepah Hills, Esmeralda Co., Nevada. E457900, N4210500, 1880 m. 7 August 1994. *M. californicus* (2 males, 1 nonreproductive female, 1 post-lactating female), *P. hesperus* (1 lactating female, 2 nonreproductive females, 1 post-lactating female), *C. townsendii* (1 male, 2 post-lactating females).
18. Fish Lake Valley Hot Springs (S), Esmeralda Co., Nevada. E413500, N4190400, 1470 m. 26 June 1994. *E. maculatum* (audible detection).
19. Mine adits near Tarantula Springs, Silver Peak Range, Esmeralda Co., Nevada. (a) E436300, N4183400, 2070 m. 2 January 1995. *C. townsendii* (1 hibernating). (b) E437200, N4183100, 2160 m. 2 January 1995. *P. hesperus* (1 hibernating), *C. townsendii* (2 hibernating). (c) E437200, N4183100, 2161 m. 2 January 1995. *C. townsendii* (1 hibernating). (d) E437500, N4183500, 2100 m. 2 January 1995. *C. townsendii* (1 hibernating).
20. Mine adit near Lida, Esmeralda Co., Nevada. E459300, N4143200, 1812 m. 26 February 1995. *M. ciliolabrum* (1 hibernating).
21. Mine adits near Dry Creek, White Mountains, Esmeralda Co., Nevada. (a) E390700, N4190300, 2220 m. 3 January 1995. *C. townsendii* (4 hibernating). (b) E390300, N4190600, 2270 m. 3 January 1995. *M. ciliolabrum* (1 hibernating). (c) E390100, N4190600, 2260 m. 3 January 1995. *C. townsendii* (1 hibernating), *M. ciliolabrum* (2 hibernating). (d) E390200, N4190800, 2220 m. 3 January 1995. *C. townsendii* (2 hibernating).
22. Mine adits near Coyote Springs, Silver Peak Range, Esmeralda Co., Nevada. (a) E436200, N4180400, 1800 m. 4 January 1995. *C. townsendii* (1 hibernating). (b) E436200, N4180500, 1800 m. 4 January 1995. *C. townsendii* (1 hibernating), *M. ciliolabrum* (2 hibernating).
23. Mine adit near Upper Indian Springs, Bullfrog Hills, Nye Co., Nevada. E515700, N4089400, 1500 m. 24 February 1995. *C. townsendii* (2 hibernating).
24. Mine adits near Old Camp, Gold Mountain, Esmeralda Co., Nevada. (a) E470200, N4124300, 1980 m. 26 February 1995. *P. hesperus* (1 hibernating), *C. townsendii* (8 hibernating). (b) E472700, N4123100, 2170 m. 26 February 1995. *C. townsendii* (2 hibernating).
25. Blue Dick Mine, Palmetto Mountains, Esmeralda Co., Nevada. E450600, N4145700, 2460 m. 26 February 1995. *P. hesperus* (2 hibernating), *C. townsendii* (7 hibernating).
26. Mine adits near Marietta, Excelsior Mountains, Mineral Co., Nevada. (a) E380800, N4237200, 1945 m. 30 December 1994. *M. ciliolabrum* (3 hibernating), *C. townsendii* (1 hibernating). (b) E380500, N4237600, 1950 m. 30 December 1994. *M. ciliolabrum* (2 hibernating), *C. townsendii* (7 hibernating). (c) E382300, N4234600, 1625 m. 31 December 1994. *M. ciliolabrum* (1 hibernating). (d) E381400, N4234200, 1560 m. 31 December 1994. *C. townsendii* (1 hibernating).

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[a] Habitat type (see Table 2)

[b] Universal Transverse Mercator (UTM) coordinates

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HISTORY OF THE NAMING OF THE FERRUGINOUS HAWK

Neil D. Woffinden[1]

ABSTRACT.—The Ferruginous Hawk, a breeding bird endemic to North America, was named *Falco ferrugineus* in 1838 by H. Lichtenstein, curator of the Berlin Zoological Museum. The type was collected by F. Deppe near present-day Monterey, California. In 1844 G.R. Gray of the British Museum assigned the name *Buteo regalis* to a Ferruginous Hawk specimen of unknown origin, but perhaps donated to the museum by John Phillips, a renowned British geologist. The species was known as *Falco (Buteo) ferrugineus* until the 1920s when it was discovered that this epithet was occupied. The next name in priority was Gray's *Buteo regalis*, which then became valid. The species has been known by a number of common names. Even though any reference to the rusty brown markings on the otherwise white plumage is no longer part of the species scientific name, the Ferruginous Hawk continues to be the most frequently used common name.

Key words: Ferruginous Hawk, Buteo regalis, *scientific name, history.*

The Ferruginous Hawk (*Buteo regalis* Gray 1844) is a large prairie buteo of western North America. It breeds from eastern Washington, southern Alberta, and southern Saskatchewan south to eastern Oregon, Nevada, northern and southeastern Arizona, New Mexico, north central Texas, western Oklahoma, and western Kansas (American Ornithologists' Union 1983). Wintering from Montana through southern California to northern Mexico, the species occasionally reaches the arid highlands of central Mexico (Peterson and Chalif 1973, Root 1988, Bechard and Schmutz 1995). As a winter resident it is mostly absent from the Great Plains and the lower altitudes of the Imperial Valley regions inland from Monterey Bay. Two wintering concentrations occur, one southwest of the Davis Mountains and along the Rio Grande valley in Texas, and another from Amarillo and Dalhart, Texas, through northeastern New Mexico and the panhandle of Oklahoma along the New Mexico–Texas border. With the exception of the latter 2 areas, the species is uncommon throughout most of its wintering range (Peterson and Chalif 1973, Root 1988, Bechard and Schmutz 1995).

This large, temperate-zone species possesses feathered tarsi as does its smaller and more northerly distributed congener, the Rough-legged Hawk (*Buteo lagopus*). Although not closely related, both species were called "roughlegs" for many years. In an attempt to reduce confusion, *Buteo regalis* for a time was called the Ferruginous (from the Latin *ferrugineus*, resembling iron rust in color) Rough-legged Hawk, and *B. lagopus* (from the Greek *lagos*, hare, and *pous*, foot, or hare-foot) the American Rough-legged Hawk. The confusion continued, however, and subsequently the reference to "feathered tarsi" was dropped for *B. regalis.* It is simply known now, in reference to the rusty brown markings on this otherwise light-colored bird, as the Ferruginous Hawk. A melanistic phase also occurs in the species. Some dark birds are strongly washed with rufous and are variously called the "red," "rufous," or "erythristic" phase (Palmer 1988).

Endemic to a limited area of North America and Mexico, the species was first collected and named by German and British workers. One specimen was collected, apparently at Monterey, California, by Ferdinand Deppe in 1836 during his return to Germany from one of his collecting trips to Mexico (Stresemann 1954). Heinrich Lichtenstein (1839), curator of the Berlin Museum of Zoology, made this specimen the type of his *Falco* (=*Buteo*) *ferrugineus,* but the name was preoccupied (Stresemann 1922). Another specimen, given to the British Museum by a Mr. John Phillips, was assigned the name *Buteo regalis* by George Robert Gray (1844), the museum's assistant keeper of birds. This specimen was from Monte del Real, Hidalgo, Mexico, and could have

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been collected by William Bullock, Jr., or F. Deppe. Both Bullock and Deppe were collecting natural history specimens in tropical eastern Mexico during this time (Stresemann 1954, Bullock 1971).

Finally, Andrew Jackson Grayson, an American painter and naturalist, named the species *Buteo californica* based on a specimen collected and painted in 1857 near San Jose, California (Grinnell 1932).

Remarkably, both F. Deppe and the Bullocks, who collected in Mexico at the same time, met, and Bullock Jr. accompanied Deppe on a number of collecting excursions. It is interesting that Deppe, who collected almost exclusively in Mexico, nonetheless obtained the type of Lichtenstein's *Falco ferrugineus* at Monterey, California, where he (Deppe) spent little time, presumably occupied in business and preparing to ship out. Is it possible that he had obtained the hawk at Monterrey, Mexico, and brought it to California with him as he prepared to return to Germany? As a winter visitor the Ferruginous Hawk might occur in either of these 2 areas.

It is also of interest that all 3 collectors involved with naming the Ferruginous Hawk, the Bullocks, Deppe, and Grayson, knew it only on its winter range and in areas where, even in those days, it must have been uncommon or perhaps a straggler.

NAMING OF THE SPECIES

On 24 December 1836 Ferdinand Deppe, a German with ties to Heinrich Lichtenstein, curator of the Zoological Museum of the University of Berlin, shot a hawk near Monterey, California, which was then part of Mexico. The specimen was acquired by the Berlin Museum and Lichtenstein (1839) made it the type of the species *Falco ferrugineus*.

During this era the Berlin Zoological Museum was routinely receiving specimens, many of which were unique, from collectors working throughout the world. As new specimens arrived, Lichtenstein gave every species, or what he judged to be a species, a name. This was done primarily for his own convenience, to give the specimens a distinguishing mark for his personal need, and without consulting the literature. Although the names were used in Lichtenstein's registers and reappeared on labels of the mounted specimens, Lichtenstein rarely published them in connection with a scientific description (Stresemann 1954). Even though *Falco ferrugineus* was an exception, true to form, Lichtenstein failed to check the name for availability. Had he done so, he perhaps would have noted that it had been used previously for another species.

In 1835 Alexander von Nordman, professor of zoology and botany at Odessa Botanical Institute, Ukraine, USSR (currently part of the Odessa I. I. Mechnikov State University), had described a raptor from Brazil (Nordman 1835), assigning it the name *Falco ferrugineus*. Ironically, the specimen Nordman made the type of his *Falco ferrugineus* was in fact a Tiny Hawk (*Accipiter superciliosus*), which had been named by Linneaus himself nearly a century earlier (Stresemann 1922). As Nordman's *Falco ferrugineus* was itself a synonym, it also became an invalid name. It is interesting, however, that even though *ferrugineus* was dropped from the scientific name, the common name has remained the Ferruginous Hawk. So, when Lichtenstein named the Ferruginous Hawk *Falco ferrugineus* in 1838, based on the specimen from Monterey, California, the name was preoccupied by 3 yr. Nevertheless, Lichtenstein's name was long used in the combination *Buteo ferrugineus*, as it was 1922 before the preoccupation was noted (Stresemann 1922). Since *Falco*=(*Buteo*) *ferrugineus* was a synonym of an earlier name, the valid name for the Ferruginous Hawk had to be the next available.

In 1841 a Mr. John Phillips of Duke Street, London, referred to by Sharpe (1874) as John Phillips, Esq., but otherwise unknown, donated 11 bird skins to the British Museum. The only information presented with the skins was that 6 of the group, 1 of which was a raptor, came from Real del Monte, Hidalgo, Mexico. Three years later G.R. Gray (1844), assistant-keeper in charge of birds, named the single raptor *Buteo regalis* (from the Latin *regalis*, relating to or suitable for a king). Subsequently, with the invalidation of Lichtenstein's *Falco ferrugineus* as a result of Nordman's earlier use, *Buteo regalis* became the valid name of the species.

The species was also named *Buteo californica* by Grayson in 1857, based on a specimen he probably collected in the fall of 1856 near San Jose, California (Grinnell 1932). However, as this name followed Gray's *Buteo regalis* (1844), it could not be valid. Other synonyms

(Friedmann 1950) include *Archbuteo regalis* (1844), *Lagopus ferrugineus* (1844), *Archbuteo ferrugineus* (1848), *Buteo ferrugineus* (1919), and *Triorchis ferrugineus* (1922).

COMMON NAMES

Buteo regalis has been widely known as the Ferruginous Hawk for more than a century. McAtee (unpublished microfilm) lists a number of other common names used less frequently: California Squirrel Hawk, Ferrugineous Buzzard, Cacique, Eagle Hawk, Rusty Hawk (also Banks 1988), Western Rough-legged Buzzard, and White-breasted Squirrel Hawk. Local names, apparently in reference to the dark phase, include Black Hawk (Utah); Black Mexican Eagle, Black Spanish Eagle (Texas); also, Chap Hawk (Alberta, apparently in reference to the feathered condition of the legs); Chicken Hawk; Gopher Hawk (Manitoba, Kansas); Prairie Eagle (Kansas, Saskatchewan, California); and Squirrel Hawk (Colorado, New Mexico, Washington, Oregon, and California). French names include buse pattue couleur de rouille (rust-colored feather-legged buzzard), buse pattue ferrugineuse (same as previous), and buse rougeatre (reddish buzzard), all referring to the reddish or rusty coloration of the light phase. German and Spanish names refer to its size (Konigsbuzzard [del Hoyo et al. 1994], king buzzard; aquililla, small eagle), appearance (busardo herrumbroso [del Hoyo et al. 1994], rust-colored buzzard; aquililla patas asperas [Bechard and Schmutz 1995], rough-legged buzzard or small eagle), or distribution (gavilan serrano, mountain hawk).

COLLECTORS AND TAXONOMISTS

The Bullocks

Mexico's independence from Spain in 1821 made it possible for Europeans to settle in Mexico and to send parcels home. As early as 1823 William Bullock, Sr., went to Mexico to, in his words, "acquire scientific information" (Bullock 1971). Bullock, a London goldsmith and owner of the "London Museum," a private collection of both art and natural history pieces (which, prior to his travels, he had been forced to dispose of through an auction to satisfy creditors), collected widely in addition to securing some mining interests while in Mexico. Returning to London at the end of 1823, he exhibited a variety of New World artifacts along with a few Mexican birds and mammals in a public showing entitled "New Spain" (Stresemann 1954).

Bullock and his son, William Bullock, Jr., disembarked in the New World at the city of Veracruz. Bullock Sr. described his experiences in the book *Six Months Residence and Travels in Mexico*, published in 1824 and reprinted in 1971. It is worth quoting at some length, since his adventures provide insight into the difficulty of travel but the apparent ease of obtaining scientific specimens in mid-19th–century Mexico.

The Bullocks soon found that glowing accounts they had read regarding travel in Mexico were gross exaggerations. Following an initial stroll around the Veracruz city square, Bullock states:

> [W]e returned to our hotel, if such it deserved to be called, where we could not even be accommodated with beds. With some difficulty I procured a kind of bedstead, on the sacking of which a sheet was spread, and over that a small piece of baiza: this constituted the whole furniture of the room, which had no window, but only an opening that communicated with a billiard room, whose noisy visitors were alone, sufficient to prevent repose. On preparing to lie down, I discovered that the solitary sheet was absolutely wet; yet upon making my complaint to the landlord, he replied, that he knew it, but that he had no other. I told him that wrapping myself in my great coat, and sitting in a chair all night, would be preferable to such a bed; to which he rejoined with the utmost *sang froid*, that he thought it would, and left me to pass a sleepless night, tormented with noise, heat, and mosquitos.

Bullock Sr., his son, a servant, and a Frenchman soon departed Veracruz for Jalapa, a distance of approximately 100 km. The surroundings were inhospitable and travel was slow; it took them 4 days to make the journey. Toward the end of the 1st day they stopped

> to take some refreshment at a place consisting of a few huts, called Santa Fe; where I shot several birds, among them the crested Meadow-Lark of America, a large and fine bird for the table; these were as tame as fowls in the poultry-yard. Through the rest of the evening the birds, hares, &c. were very numerous, and we might easily have killed sufficient for a large party. The hares are very small; considerably less than our rabbits, but in other respects like our own. The country, too, began to be improved by vegetation before we arrived at San Rafael, where we were to pass the night.
>
> Here we found nearly as good an inn as any on the road, and a description of it and our treatment, may serve as specimens of the whole, no doubt to the surprise of those who have believed what some writers,

> not travellers, have asserted respecting the ample accommodations to be found in these parts. The Posada, is a large shed thatched with leaves or reeds, partly enclosed, like a bird-cage, and freely admitting the air;—so little barricaded as to allow whatever passes within to be seen from without;—and the roof projection very considerably over the sides. Under this projection, and in the open air, several travellers had laid themselves down for the night. Our baggage was placed in the interior: and when we inquired where we were to lodge, we were conducted to the same place, and told that unless we had beds of our own we must repose on the floor; indeed nothing was furnished but shelter from the rain, and Indian corn for the cattle. For ourselves, we with difficulty procured some planks on which to place our mattresses, and after making a scanty meal of what we had brought, for bad water and a little bread were all the house afforded, we prepared to go to rest, hoping that the fatigue we had gone through would act as a soporific. Several persons of both sexes, with some children, were in the same room with us, in a sort of gallery that projected over the enclosure. Our mules and those of other travellers were fastened on the outside, while numerous dogs belonging to the house, as well as those attached to the different conveyances of the travellers, were mingled with their masters, and kept up such a barking as to render sleep impossible. We had horses close to our heads, eating Indian corn; the mules kicking and fighting; the muleteers cursing; intolerable and suffocating heat; braying of asses; singing and stinging of mosquitos, and the biting of myriads of fleas completed the *comforts* of what has been called an inn. How did I pray for a glass of water to moisten my parched and feverish lips; how did I long for an English barn or hay-loft; either had been a Paradise to such an *infernal* spot. To leave it, however, would have been to have run the risk of being devoured by the surrounding dogs. Day-light at length brought us relief, and, clearing our persons from the deposits of the poultry that had roosted over our heads, we reloaded our carriage, and proceeded on a better road than heretofore, having in some parts been carried, at considerable labor and expense, over morasses which would otherwise have been impassable (Bullock 1971).

A number of specimens, including several raptors, were collected before the group reached Mexico City, where numerous artifacts were added to the growing collection. Bullock's travels resulted in a book and a collection of materials that were the basis of the London display, both mentioned previously.

Ferdinand Deppe

Accounts of European travelers in Mexico, upon reaching Germany, excited the curiosity of a wealthy nobleman, the Count von Sach, "Zweiter Ober-Jagermeister" and chamberlain to the King of Prussia. Following a successful collecting trip to Egypt and Cyprus, he desired to visit Mexico, provided a collecting naturalist of good reputation could accompany him (Stresemann 1954). Heinrich Lichtenstein, director of the Zoological Museum of Berlin University, recommended Ferdinand Deppe, who was at the time a gardener with the Royal Gardens but had a close association with the Zoological Museum. Deppe gave up his job in 1821 and prepared for the voyage to Mexico by perfecting bird and mammal skinning techniques, studying English and Spanish, and reading extensively on the zoology, botany, and geography of South America. The Count, apparently in no hurry to leave, delayed their voyage for 3 yr when finally, at the insistence of Deppe, they at last departed, reaching London in August 1824. An extended delay allowed Deppe an opportunity to visit Bullock's Mexican show, the British Museum, and private shops dealing in Mexican specimens.

Departing England in October, the group reached Alvarado, Veracruz, Mexico, in mid-December. Apparently not able to get along, the Count and Deppe separated in May 1825, with Deppe completing the remainder of the expedition at his own risk. During the 2 yr of his initial Mexican collecting stint, he traveled to Mexico City and back to Veracruz, where on the return trip, Deppe made the acquaintance of William Bullock, Jr., who had remained in Mexico when his father returned to England. The pair collected extensively during their several-month association. For instance, in the years 1825 and 1826, Deppe alone made 958 bird skins (representing about 315 species) and collected a number of mammals, reptiles, amphibians, fishes, and snails, thousands of insects, and a wealth of botanical material.

Supposedly, all of Deppe's zoological materials were bought by Lichtenstein and the Zoological Museum of Berlin (Stresemann 1954). However, in August 1826, William Bullock, Sr., who had returned to Mexico as director of a British mining company that he had founded following his 1st visit, joined Deppe and Bullock Jr. in Temascaltepec. Returning to London in September of that year, Bullock Sr. took with him many bird skins, and perhaps other materials, which apparently had been collected cooperatively by the pair (Stresemann 1954). This was the 2nd time materials collected by the Bullocks were carried to Great Britain and perhaps the 1st opportunity for Deppe to send his materials somewhere other than the Berlin Museum.

Deppe departed from Veracruz in April 1827 and, although welcomed back to Berlin, was not awarded a hoped-for post with one of the scientific institutions of the city. Disappointed, he returned to Mexico the following year accompanied by a botanist friend Wilhelm Schiede. The pair hoped to make a living by selling zoological and botanical specimens to European museums and dealers. In the meantime, however, the Berlin Museum had fallen on hard times financially, thus making it impossible for Lichtenstein to buy additional Mexican material.

Unable to dispose of their specimens, Deppe and Schiede were forced to give up collecting in 1830. Schiede died a short time later and Deppe, to survive, became a commission agent for merchants located at Acapulco, Mexico, and Monterey, California. His position took him throughout the western and northern states of Mexico until 1836, when, having been cheated out of all his assets, he decided to return to Germany. On 24 December 1836, during his return journey, he collected the specimen that Lichtenstein made the type of *Falco ferrugineus* near Monterey, California. Arriving in Berlin in 1838, he was again denied an appointment and died in oblivion in 1860 (Stresemann 1954).

Heinrich Lichtenstein

Martin Karl Heinrich Lichtenstein was born in Hamburg in January 1780. He studied medicine and received the degree Doctor of Medicine and Philosophy in 1802, following which he traveled to South Africa as the private tutor of the newly appointed governor's teenaged son and the family's medical attendant. The governor, anxious to view the colony firsthand, explored the area extensively shortly after arriving. Lichtenstein accompanied the group as the medical officer and, since he was already an ardent naturalist, collected numerous specimens and made careful observations throughout the journey. The account of his 4 yr in Africa is recorded in his 2-volume work, *Travels in Southern Africa* (Lichtenstein 1928).

Upon the cession of the Cape to the English in 1806, Lichtenstein returned to Germany, where he occupied himself with the arrangements of his collections and manuscripts. In 1811 he received an appointment as professor of zoology at the University of Berlin. Two years later he assumed the directorship of the Zoological Museum (Lichtenstein 1928), which under his care became one of the greatest in Europe. He also founded the Zoological Garden in Berlin, which, despite numerous obstacles, succeeded because of his leadership. The garden boasted an exotic collection of live animals that thrilled the viewing public of that day (Stresemann 1960).

In spite of his many positive attributes, Lichtenstein failed to pay sufficient attention to detail in his taxonomic activities. He often considered some specimens as "new species" when they were not, while frequently trading or selling unique specimens as duplicates. He never properly studied the vast quantities of avian study skins sent to the Berlin Museum by Deppe and others. Critical examination of this material was left to learned visitors at the museum and subsequent curators (Stresemann 1960). Although, as stated previously, he assigned scientific names to numerous specimens, only a few were published. Also, because he failed to check the literature for availability, his names were often preoccupied, as was the case with the Ferruginous Hawk.

His shortcomings in this area, which have been widely criticized, unfortunately have overshadowed his many accomplishments. He conducted numerous excursions throughout Europe during his lengthy tenure at the University of Berlin and continued, until his death at age 77 in 1857, as a lecturer of zoology (Stresemann 1960).

Considering Lichtenstein's unwise disposition of unique materials and the destruction of many specimens during the Second World War, it is fortunate that the type specimen of *Falco (Buteo) ferrugineus*, a female "mount" in good condition, still exists in the Zoological Museum of the present-day Humboldt University in Berlin (G. Maurersberger 1990 personal communication).

WHERE WAS THE DEPPE SPECIMEN COLLECTED?—For a time it was thought that the specimen Lichtenstein made the *B. ferrugineus* type was collected at Monterrey, Mexico (Palmer 1988: 407). But Stresemann apparently found that Deppe had never been in Monterrey, Mexico; thus, he concluded that the type locality must have been Monterey, California, the site of Deppe's last embarkment for Europe.

We know that Deppe sailed from Monterey, California, instead of Veracruz, Mexico, as he had done on previous trips, because he stopped in Oahu, Hawaii, and joined the renowned American ornithological collector J.K. Townsend in January 1837. At least 2 of the species represented in their 1837 collection subsequently became extinct and are known only from their specimens (Olson and James 1994). Stresemann (1954) intended to write a paper dealing with the events of the Hawaiian collections, which may have provided additional information concerning the collection of the Deppe specimen. Unfortunately, it was not completed before his death. Deppe can be unquestionably placed at Monterey, California, in December 1836, and so it appears that this was the locality for the *B. ferrugineus* specimen.

G.R. Gray

Meanwhile, a Mr. John Phillips of Duke Street, Adelphi, London, presented 11 bird skins to the British Museum in 1841. No information is available as to how the skins came into Mr. Phillips's possession; at present we are not even certain of his identity. Six of the specimens reportedly came from Real del Monte, Hidalgo, Mexico, but no collection date was given. One of the 6 was a Ferruginous Hawk; it was described as *Buteo regalis* by George Robert Gray, an assistant-keeper in charge of birds and a brother to J.E. Gray, keeper of the Zoological Department for 34 yr. Energetic and dedicated to the building of the Zoological Department, J.E. Gray was responsible for the immense growth of collections during a time when British science otherwise was underfunded.

G.R. Gray, of a much quieter temperament, was totally different from his brother. Working assiduously, he processed large amounts of material in a precise manner. He has been characterized as a "thoroughly conscientious clerk" (Sharpe 1906). However, he had little knowledge of birds in the field. A story is told of his succumbing to the pressures placed upon him by others who continually reminded him of this deficiency. One day he rented a gun and went into Hertfordshire to shoot birds. Promptly arrested by a gamekeeper for trespassing, he quickly terminated the endeavor. Despite his lack of knowledge concerning birds in life, he was immensely acquainted with bird skins and proper systematic rules. As a result, the British Museum possessed a well-named collection (Sharpe 1906).

G.R. Gray was born in 1808, educated at the Merchant Tailors' School in London, and at an early age assisted Mr. J.G. Children, a keeper at the museum, in the arrangement of an extensive collection of insects. He published various works on insects including an account of species that are parasitic on other insects. His "List of the Genera of Birds," which contained 1065 genera, including the type species on which each genus was founded, was published in 1840. The following year he revised and expanded the list to 1232 genera. Other works followed, which were of great importance to ornithologists of the day and were carefully accurate, as "the author was indefatigable in his researches, and spared no pains in searching out all that had been done in ornithology from every available source" (Babington et al. 1872). He appeared to have been intolerant of criticism both in his professional and private life but was characterized, perhaps by his brother, as a person of true heart and a dedicated friend. He died 6 May 1872 at the age of 64 while actively pursuing his work (Babington et al. 1872).

Due to the preoccupation of Litchenstein's *Falco ferrugineus*, Gray's *Buteo regalis*, next in order, became the valid name for the Ferruginous Hawk.

A.J. Grayson

The species was also named *Buteo californica* by Andrew Jackson Grayson (Hellmayr and Conover 1949). A colorful and eventually rather tragic figure, Grayson (1818–1869) was born and raised in northern Louisiana, but a yearning for the West led him, at age 28, to help organize a wagon train to California. He reached the Golden State in October 1846, accompanied by his wife and 2-yr-old son. In 1853 Frances Grayson took her husband to see the recently acquired set of Audubon's "Birds of America" at San Francisco's Mercantile Library. Grayson was enthralled and, although he lacked training, determined that he would paint all the birds of the Pacific slope unknown to Audubon. Teaching himself to paint, he corresponded with and was encouraged on his mission by ornithologists at the Smithsonian Institution.

Eventually, the Graysons settled in Mexico, where he painted in earnest, collected numerous specimens that he sent to the Smithsonian, and thoroughly described the avifauna of some areas, including, at the time, the undisturbed Soccoro Islands. While in Mexico, the Graysons were involved in a variety of adventures including shipwrecks and robberies. Following the unexplainable murder of their son, Grayson pined inconsolably, but continued his work until he succumbed to yellow fever in 1869. After his death Frances returned to California, intent on publishing her husband's plates. Unable to raise the necessary funds, however, she eventually donated his works to the Bancroft Library of the University of California at Berkeley. Here they lay unnoticed until discovered by Lois Chambers Stone in 1949 (Graham 1987, Howell 1987). Her discovery prompted publication between 1949 and 1957 of 23 color reproductions of Grayson paintings in *The Condor.* More recently, prints of all 156 surviving paintings along with a biography and other materials about Grayson have been published in an elegant multi-volume set, *Birds of the Pacific Slope* (Stone 1986).

Since Grayson undoubtedly knew the Ferruginous Hawk in life and was a bona fide field ornithologist, it is unfortunate that his name is not the name for the species. However, G.R. Gray's *Buteo regalis* (1844) has priority because of its earlier date.

WHO COLLECTED THE PHILLIPS SPECIMEN?

No collector was listed for the specimen that J. Phillips donated to the British Museum and G.R. Gray made the type of *Buteo regalis.* It is tempting, however, to speculate as to its origin. The Bullocks and Deppe were the 1st collectors of birds in Mexico (Stresemann 1954). It appears from Bullock's writing (Bullock 1971) that they amassed a sizeable collection. For instance, on one occasion Bullock Sr. records that he had collected nearly 200 specimens of hummingbirds alone during the 6 months of his 1st visit (Bullock 1971:273). While traveling to Mexico City in March 1823, Bullock reported, "The birds throughout this day's journey were very tame, and we shot some, but as we had no means of preserving them, they were lost." During the journey the group "saw many different species of eagles, numerous and beautiful hawks, various crows, oriole, cuckoos,—all of which suffered us to approach within pistol shot" (Bullock 1971:36–37). Nearing Perote, Veracruz, they "saw several specimens of eagles, hawks, and other birds of prey, some of which came so near our carriage as to be easily shot without our getting out" (Bullock 1971:75). On the return trip to Veracruz in July, also near Perote, 2 vultures and several hawks were shot, again from the coach window (Bullock 1971:450). In addition to his extensive collection of skins and other specimens, Bullock had, in his own words, a "menagerie" of living animals including "several armadillos, deers, parrots, currassow-birds, quans, tiger-cats, and etc." that he was taking back to England with him at no expense on the British ship *Phaeton* (Bullock 1971:483).

Although Bullock's collection undoubtedly contained numerous raptor specimens, since his visit was from March to July, it is unlikely that any of the birds he reportedly shot would have been Ferruginous Hawks. However, the younger Bullock and Deppe actively collected in the same area for more than 2 yr. They collected extensively around Mexico City as well as the area between Jalapa and the capital during various trips. Depending on the route traveled, they could have passed through Hidalgo on one of their journeys from Jalapa to and from Mexico City as Real del Monte is only approximately 100 km northeast of the city center. In addition, Deppe made several excursions out of Jalapa and could have reached Real del Monte by traveling 200 km in a northwest direction. Thus, it is likely that they encountered wintering Ferruginous Hawks during their travels.

Although the Phillips specimen cannot be traced to Deppe and Bullock, as mentioned previously, Bullock Sr., upon his return from his 2nd trip to Mexico, carried a number of specimens with him to England, which had been collected by his son while in the company of F. Deppe. It is also possible that he took with him specimens that Deppe had collected independently. Stresemann (1954), however, states that the Bullock New Spain exhibit contained only a few birds and mammals arranged on native plants. What became of the rest of his sizeable collection? Had it been sold or placed on consignment in private shops? Was the collection still in Bullock's possession but not displayed? Did William Swainson receive some of it, or had it at least passed through his hands? Even though the answers to these questions are not available, it is likely that

Mexican specimens collected by the Bullocks were held privately at the time J. Phillips made his donation to the British Museum.

Also, it is usually thought that the Berlin Museum received all of the Deppe Mexican materials, but, as pointed out previously, the museum was unable to buy all of the Deppe/Shiede specimens. In an attempt to find other markets at this time, Deppe's brother published lists of available specimens and distributed them throughout Europe. The number of specimens disposed of in this effort was apparently modest, as the earnings were insufficient to support continued collection. However, some of Deppe's materials, perhaps including the *B. regalis* type, were distributed to locations other than Berlin at this time.

It is possible that J. Phillips collected the specimen himself. However, as there is no record of anyone of that name in Mexico, it safely may be assumed that he was a hobbyist who acquired only a few Mexican birds which he later gave to the British Museum.

Although we do not know who collected the Phillips specimen, Mexican specimens collected by the Bullocks and Deppe were likely privately held at the time the *Buteo regalis* type was donated to the British Museum. Since the Bullocks and/or Deppe did collect hawks in Mexico, and the whereabouts of much of their vast collections cannot be accounted for, probably 1 of the 3 collected the *Buteo regalis* type.

John Phillips

The only information available on John Phillips is his address and a reference to him as J. Phillips, esquire. Apparently, he was a professional person who donated a group of various bird skins to the British Museum. He must have felt his specimens were of value to the museum but was probably not an ornithologist since there was no pattern to his collection. It is also highly unlikely that he would have collected such a limited number of diverse specimens had he visited Mexico and done the collecting personally. So, it appears that John Phillips was familiar with scientific collections, felt that the British Museum would be an appreciative recipient of his specimens, but had not personally collected the Mexican birds.

A check of the 1841 British census failed to find a J. Phillips on Duke Street in London. John Thackery, currently an archivist at the Natural History Museum, stated that there was an active collector for the museum in the 1840s by the name of John Phillips. This Phillips was a geologist. When Thackery was told that the Phillips of interest resided on Duke Street in the Adelphi section of London, he suggested that this would be a likely location in which a professor at London University might reside. Was John Phillips, geologist and museum collector, the John Phillips who donated the *B. regalis* type to the Museum? It seems likely for the reasons stated previously.

John Phillips, geologist, was born 25 December 1800. Orphaned at the age of 8, Phillips was raised by his uncle, William Smith. Smith, a geologist of note, was widely known as "the father of English geology." Soon after Phillips took up residence with his uncle, he developed a keen interest in geology. The boy and his uncle became inseparable for several years, and Phillips's knowledge of geology and paleontology flourished under the tutelage of his accomplished guardian. Because of his achievements, while accompanying his uncle on a lecture series to York in 1825, he was offered the position of keeper of fossils in the York Museum. In 1834 Phillips was elected a Fellow of the Royal Society and accepted the Professorship of Geology in King's College, London, a post he held for 10 yr. His next position was professor of geology at Trinity College, Dublin. He left Ireland in 1853 to join the faculty at Oxford. A professor of geology at Oxford, he also served as keeper of the Ashmolean Museum from 1854 to 1870. He published widely not only on geology but also astronomy and meteorology. John Phillips died at the age of 74 as a result of an accidental fall down a stone staircase.

Was John Phillips, the geologist, the John Phillips who donated the *B. regalis* type to the British Museum? The evidence is inconclusive, but it certainly doesn't rule him out.

Although some questions remain concerning the Deppe and Phillips specimens, events surrounding the collection and naming of the Ferruginous Hawk make an interesting addition to current literature on this splendid bird.

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ECOLOGICAL REVIEW AND MANAGEMENT RECOMMENDATIONS FOR RECOVERY OF THE ENDANGERED GILA TOPMINNOW

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ABSTRACT.—Ecology of the endangered Gila topminnow is reviewed, described, and reconstructed; natural conditions are placed in perspective with human-altered habitats of today. In the natural state of waxing and waning of habitat size as a function of precipitation patterns and catastrophic events such as severe winter cold, the species in the past likely underwent dramatic expansions and contractions in population size and geographic range. Today, population expansions are unlikely because of constraints imposed by human activities. The original patterns of dispersal from refugia in "good" times and retreat in "bad" times, if they are to occur, must be re-created through human translocation. Further, most refugia now are destroyed or inaccessible to recolonization, so remnant, natural populations, along with established, transplanted stocks of appropriate size and genetic quality, need protection. Populations also must be established and maintained in artificial refugia. Last, even if connectedness were to be reestablished and refugia provided, intervening habitats harbor introduced piscivores such as western mosquitofish that interdict and eat dispersing topminnows and their progeny. Elimination, exclusion, or management against such offending species is mandatory to prevent topminnow extinction and achieve recovery.

Key words: Gila topminnow, Poeciliopsis occidentalis, *Colorado River, western North America, endangered species, management, recovery.*

At the time of its discovery in the mid-1800s, the small, livebearing Gila topminnow, *Poeciliopsis occidentalis* (Baird and Girard), was widely distributed below ~1600 m elevation in the Gila River basin of Arizona and New Mexico in the United States, and in northwestern Sonora, México (Hubbs and Miller 1941). It now is extirpated from much of its range in the United States, persisting naturally in only a few isolated springs and stream segments (Fig. 1), and is listed as endangered by the U.S. Fish and Wildlife Service (USFWS 1994). Although more secure in México (Hendrickson et al. 1981), both this and the closely related *P. sonoriensis* (Girard) also are declining there (Campoy-F. et al. 1989, Varela-R. et al. 1992) and are listed (collectively as *P. occidentalis*) as threatened by the Mexican Secretaria de Desarrollo Social (SEDESOL 1994). I consider *P. sonoriensis* a full species (rather than a subspecies of *P. occidentalis*) based on data presented by Quatro et al. (1996).

Disappearance of the Gila topminnow is attributable to changes stemming from human activities. Before the 1800s, livestock grazing and timber harvest began to alter natural vegetation (Hastings 1963, Hastings and Turner 1965, Bahre 1991, 1995) that changed patterns in runoff, erosion, and sedimentation. Intensive water development for irrigation commenced in the 1800s, further altering flow patterns and discharge volumes of individual streams. Even with these negative impacts, the species continued to enjoy wide distribution. In the 1940s and 1950s, however, introduction and establishment of myriad nonnative species began to change the faunas of whole watersheds by restructuring aquatic communities (Minckley 1991). A downward spiral toward extinction for Gila topminnow coincided with the establishment and spread of another livebearer, the western mosquitofish, *Gambusia affinis* (Baird and Girard).

Rauchenberger (1989) elevated *G. affinis* and *G. holbrooki* Girard, long treated as subspecies of *G. affinis*, and the nominal *G. speciosa* Girard of Texas and northern México all to full species. Common names of these fishes were changed by Mayden et al. (1992) to reflect changed taxonomy to "central" (*affinis*, formerly "western"), "eastern" (*holbrooki*, formerly "eastern"), and "western" (*speciosa*). I retain "western mosquitofish" for *affinis* on the basis of comments by Clark Hubbs (personal communication), who

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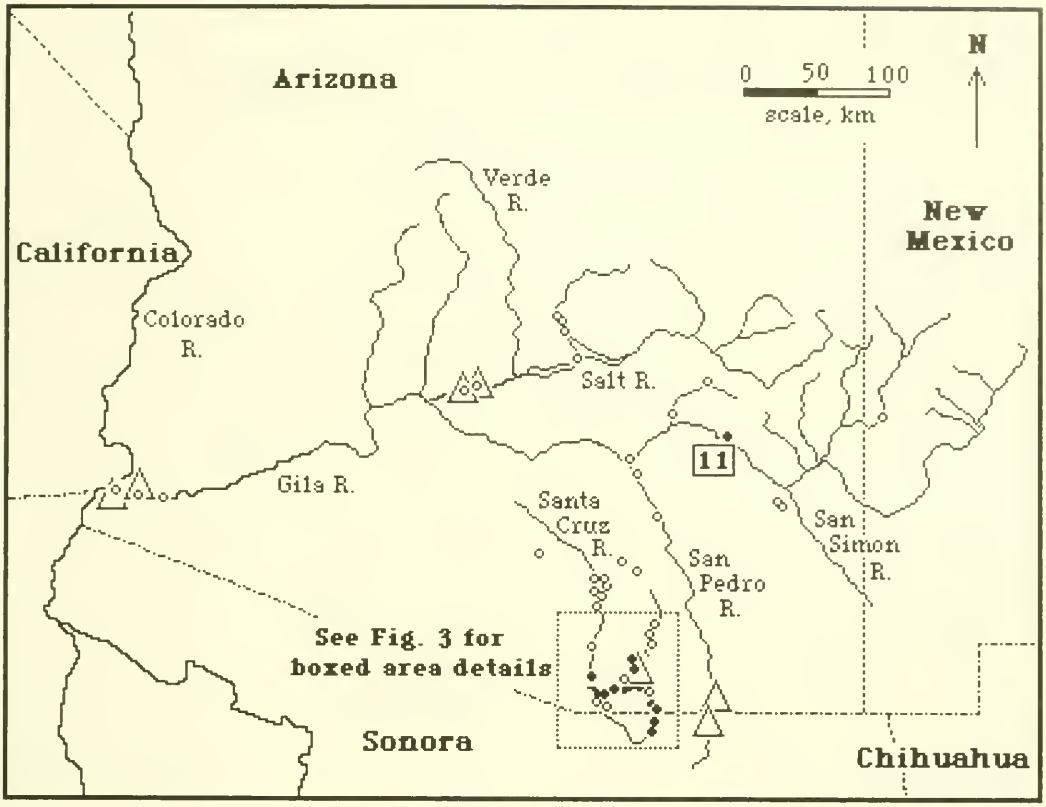

Fig. 1. Distribution of all known collection localities for natural populations of Gila topminnows in the Gila River basin, United States and México, based on museum specimens and literature records. Open circles are for extirpated populations and dots indicate collection sites between 1987 and 1997; in some instances closely adjacent sites are indicated by a single symbol. Existing populations in the United States (Table 1), with exception of Bylas Springs (indicated by the numeral 11), are boxed and shown in detail in Figure 3. Open triangles surround areas where pupfishes also were taken in times past.

pointed out that "the native range for *G. affinis* includes populations west of any *G. speciosa*. If a change is to be made, the common names should be *G. holbrooki* eastern, *G. affinis* western, and *G. speciosa* southern." "Mosquitofish," used here for all nonnative Arizona populations, refers only to *G. affinis*, based on the morphology of 423 specimens (Arizona State University [ASU] Collection; 29 localities, statewide) confirmed as this species by Taun Hoc Thai (ASU; personal communication).

Western (and/or eastern) mosquitofish have been planted worldwide in attempts to control pestiferous insects, a practice continuing today (Courtenay and Meffe 1989). The aggressive *Gambusia affinis* (Myers 1965), comparable in body size, shape, and ecology to topminnows and native to south central United States and northeastern México, was first recorded in Arizona in 1926 (Miller and Lowe 1967) and since has spread to occupy much of the region (Fig. 2). Featuring strong jaw teeth and aggressive, carnivorous feeding behavior, it was soon indicted (Miller 1961) and then convicted as an effective topminnow predator (Minckley and Deacon 1968, Schoenherr 1974, 1977, Meffe 1983a, et seq.). The native livebearer sometimes disappeared only a few short months after mosquitofish were detected (Schoenherr 1974, Meffe 1983a).

As usual, there were exceptions. First, some topminnow populations coexisted for a long time with mosquitofish before disappearing (Minckley et al. 1977), and a few still do (USFWS 1984, Abarca et al. 1994, Weedman and Young 1997). In fact, other than in 2 springs

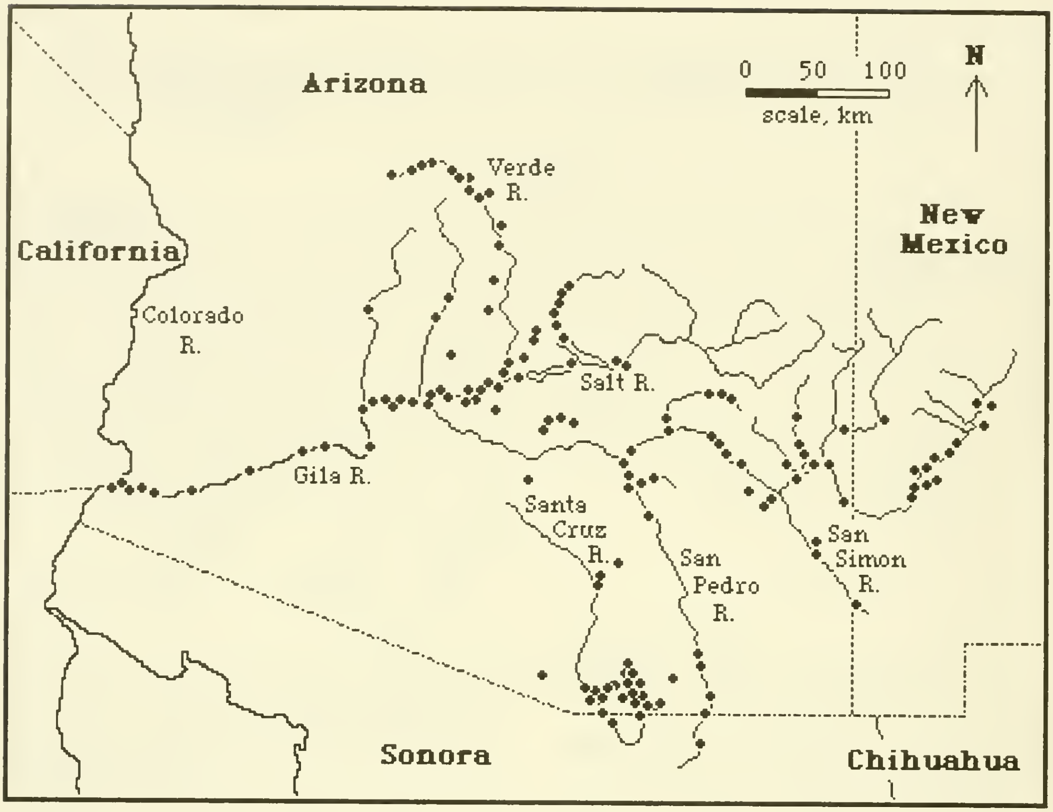

Fig. 2. Distribution of collection localities for nonnative mosquitofish in the Gila River basin, United States and México, based on ASU specimens and literature records.

and a creek where mosquitofish have not yet appeared, all 8 other natural sites where topminnows now remain are either coinhabited by or directly accessible to mosquitofish.

Second, losses of only a small proportion of translocated-then-extirpated topminnow reintroductions were attributable to mosquitofish. Of 175 sites stocked (Weedman and Young 1997), 18 (10.3%) had topminnows that survived 3–20 yr, and 157 (89.7%) failed. This rate of success was disappointingly low to some (Simons et al. 1989, Hendrickson and Brooks 1991) but seemed reasonable to others (Minckley 1995). It meant that the number of localities for wild populations had more than doubled since the effort began. At 96 sites a reason for topminnow disappearance was apparent (61 succumbed to unknown factors): 57 were desiccated, 27 were lost to flooding, 6 to winter cold, and only 1 or 2 each to mosquitofish, water quality, dredging, or livestock overuse.

The surviving, exceptional populations merit further consideration. Are there subtle factors just as dangerous as drought, flood, or mosquitofish responsible for topminnow extirpation? Should factors other than mosquitofish predation be considered in attempts to conserve and recover the species? I examined such possibilities by reviewing data for sites where topminnows occurred before and during early stages of mosquitofish establishment. I then compared these data with features at sites of long-term topminnow-mosquitofish coexistence as well as sites where translocated stocks seem to have established. Coincidence of topminnow localities with elevated winter water temperatures was far greater than expected. Thus, predation might not be the only factor involved in the Gila topminnow's demise. The possibility is examined that distribution, abundance, and persistence are also influenced by temperatures in exceptionally cold winters.

REVIEW OF GILA TOPMINNOW ECOLOGY

Life-history Features and Habitats

The Gila topminnow is short lived with high reproductive potential. Average natural life span is <1 yr, and a female bears 5–20 young at 24- to 28-d intervals (Constantz 1974 et seq.). The reproductive season varies upward to 8–9 months from spring through autumn, and may be year-round (although depressed in winter) in warm, constant-temperature springs. Females sometimes superfetate, simultaneously carrying 2 or more cohorts of young, each at different stages of embryogeny, which reduces brood intervals (Schoenherr 1974, 1977, Constantz 1980). A female also can produce multiple broods from a single insemination, perhaps throughout life (Constantz 1981, 1989). Young achieve sexual maturity in warm water in 60 or fewer days (Constantz 1976, 1979).

The Gila topminnow occupies water a few centimeters deep in slow currents, tending to concentrate in protected inlets shoreward of sandbars or debris, or associated with aquatic or streamside vegetation (Minckley 1973, Meffe et al. 1983, Forest 1992). It lived originally in a variety of habitats, from shorelines and slackwaters of rivers to small streams, springs, and marshes. It endures both intermittency and moderate floods (Meffe et al. 1983, Meffe 1984b), although severe flooding eliminated some translocated populations (Collins et al. 1981, Weedman and Young 1997). The fish is omnivorus, eating mostly detritus but also live plants and aquatic and terrestrial invertebrates (Schoenherr 1974, 1977, 1981, Gerking and Plantz 1980).

Under natural conditions Gila topminnows were largely alone in their microhabitat, encountering only larvae or juveniles of 1 or 2 other native fishes, none markedly competitive or piscivorous. Among these, only desert pupfish, *Cyprinodon macularius* Baird and Girard, likely co-occurred throughout the year; ~75% of known locales for pupfish in Arizona (before it also declined to endangered status) also supported topminnows. Pupfish were far rarer than topminnows. Only 12 samples at 8 locales were known before 1930 (Fig. 1; including the undescribed Monkey Spring pupfish, *Cyprinodon* sp.) compared with about 50 collections at approximately 20 sites for topminnows. Although physical separation between the species is minimal in shallow water, interactions are rarer in deeper habitats since pupfish remain near the bottom while, as implied by its common name, the topminnow is near the surface.

Distribution and Abundance

Under natural conditions Gila topminnows must have expanded in geographic range and population size during wetter times of maximum habitat connectedness. As habitats diminished and fragmented with drought, most populations could only have been progressively reduced in size and then destroyed, until the species was ultimately isolated into a few remaining oases fed by reliable subterranean water sources. The strategy worked because dispersal barriers vanished; topminnows then could again repopulate as soon as dry channels resumed their flow. Predisposition to exploit such a transient system through life-history and habitat-selection traits included rapid population expansion. A biological "incentive," a benefit to dispersing individuals despite danger of death from desiccation, was more food or some other factor reflected in greater reproductive output (e.g., higher fitness) as demonstrated by Constantz (1976, 1981). Not all individuals left the oases. Those that remained traded high risk with high profit in temporary waters for low-risk, low-profit survival in small, permanent habitats, thereby ensuring individual (and thus species) persistence.

Original topminnow environments were vastly different from those of today. Historically, precipitation ran more slowly off intact watersheds, and a larger proportion entered the water table. Violent floods were less frequent. Groundwater percolated downslope to fill floodplain alluvium and promote reliable baseflows in surface streams. Stream channels were geomorphically more complex, substrates more diverse and well sorted, and pools were common, scoured near tree roots, fallen logs, boulders, and banks, or behind beaver dams. Stream courses were scarcely or only locally incised. Riparian vegetation included gallery forests, dense shrublands, and riverine marshlands. Water temperature was aneliorated both in summer and winter by groundwater exchange and shading from riparian plants. In addition, no major predators other than fish-eating birds and invertebrates harassed or preyed on adult topminnows and ate their young.

Thermal Ecology

The Gila topminnow tolerates high water temperatures in summer (Heath 1962) and withstands most winter cold expected at low elevations in the Gila River basin. Nonetheless, its northern latitudinal and upper altitudinal distributional limits are apparent functions of winter water temperatures. This is no revelation since the Gila River basin is the northernmost penetration of this tropical genus (Rosen and Bailey 1963).

Low temperatures also influence the topminnow other than at the periphery of its geographic range. On 6–10 December 1978, nighttime air temperatures in much of the species' range fell to or below –6.0°C (Anonymous 1979, Jones 1979), nearly 10° lower than in a "normal" year. Such a freeze, if lasting more than 12–20 consecutive hours, proves catastrophic to many warm-adapted Sonoran Desert plants, including, among others, some life stages of saguaro cactus (*Cereus giganteus*), shrubs (bursage, *Ambrosia* spp.), trees (palo verde, *Cercidium* spp.), and other organisms as well. Such events occur only sporadically (Bowers 1980).

On 11 December 1978, I found a few hundred dead topminnows in shallow, ice-covered backwaters of Ciénega Creek, Arizona. A thermometer was not available. A few (10s of individuals) were dead in flowing water, and fewer moribund, scarcely mobile fish could be forced from shoreline beds of plants. Upstream, near a discrete spring inflow and groundwater seepage, 10s of active individuals were concentrated where ice was absent and water was 3.0–5.0°C warmer to touch. In the same stream in winter 1990, which was not exceptionally cold, Simms and Simms (1992) recorded substantial declines in topminnow abundance at 8 sites (they reported no dead fish), but not at another site near a spring inflow. Additionally, seasonal fluctuations in population size in the constant-temperature Monkey Spring (~26°C; Constantz 1976) were small compared to those in more variable environments (Schoenherr 1974, Constantz 1976, Meffe 1983a).

It is not known whether populations at warmer sites were maintained by immigration toward springs (if physically possible) or recruitment through in situ reproduction, or if declines elsewhere reflected mortality from factors other than cold. Nonetheless, of 15 pre-1930 locales (before mosquitofish were prevalent) where Gila topminnows were collected, 10 (67%) were at or within a few kilometers of groundwater-fed marshlands or known spring inflows (in part, Hendrickson and Minckley 1985), and all but 1 of the 6 northernmost sites were associated with thermal springs. The exception was Ash Creek (Jennings 1987), where I know of no springs, although that stream flows into San Carlos River, which enjoys a number of thermal inputs. Only 1 of 10 sampling sites where topminnows were absent in collections during the same time period was near a known, major groundwater inflow.

Statistics on translocated stocks show similar trends, although these data clearly are biased since spring-fed habitats (due to permanency) lacking mosquitofish (or other introduced predators) were selected for stocking. Sixteen (89%) of 18 populations that persisted 3–20 yr were in springs or spring-fed habitats. Only 48 (30.6%) of 157 places where translocation failed were at or near springs or in spring- or marshland-associated creeks, while 109 (69.5%) were where thermal amelioration either was not noted or seems unlikely (personal observation and Weedman and Young 1997).

Human Impacts

The tenuous existence of Gila topminnows has been worsened by other human interventions. Dams, diversions, other water-control structures, and long, dry reaches of stream now comprise insurmountable barriers to fish dispersal among isolated islands of suitable habitat. Even where connectedness remains, stream channels are incised and shorelines are unsuitable for survival. Groundwater tables are lowered by channel incision and further yet by groundwater pumping. Removal of subsurface water for agriculture or other purposes results in dried springs as well. Moreover, springs and other artesian outflows are often "improved" by capping, impoundment, diversion, or other means (McNatt 1979).

Even where surface water persists, stream baseflows often are reduced to a mere trickle, flowing over barren sand and gravel, distantly bordered by vertical banks, and suffering rapid heating and cooling due to exposure, low volume, and reduced groundwater exchange. Riparian vegetation is physically disrupted by floods or dies as water tables are lowered too deeply for roots to reach during drought. Flash floods are more common due to rapid runoff from denuded watersheds, and the power of flooding is concentrated downward as water rises vertically against cut banks. Both erosive and sediment-carrying capacity are greater with increased velocity in constrained channels, and transport of large sediment loads homogenizes bottoms so pools are fewer and more transient.

Furthermore, mosquitofish and other nonnative species persist and flourish in altered or artificial habitats such as livestock watering ponds, from whence they invade natural habitats, including formerly dry reaches of streams. Finally, public health agencies stock both natural and artificial waters for mosquito control as soon as surface waters reappear. Whatever the circumstances, piscivorous nonnative species appear to intercept dispersing topminnows and reduce their odds of survival to recolonize. A few instances where topminnows disappeared and did not reappear although mosquitofish were not recorded may be attributable to such interception, but also may result from interdiction by physical barriers.

TOPMINNOW-MOSQUITOFISH COEXISTENCE

Both field and laboratory evidence confirms that mosquitofish predation decimates Gila topminnow populations. The exotic has achieved an almost cosmopolitan distribution throughout and beyond former topminnow range (Fig. 2). Of natural topminnow stocks that persist (Table 1, Figs. 1, 3), 5 remained isolated from mosquitofish as of 1995–96, 2 seem to be disappearing under stress from the exotic, 3 have shared habitat for a number of years, and another (discovered in 1994; Table 1), also contaminated by mosquitofish, has appeared only since wastewater disposal recreated permanent habitat in the Santa Cruz River. What allows coexistence in these last 4 areas?

Physical Influences

Long-term coexistence has long been attributed to habitat features. Meffe et al. (1983) implied disturbance as a factor in topminnow disappearance; e.g., they ". . . persist in undisturbed habitats allopatric with mosquitofish, and decline or disappear where the exotic has invaded." Courtenay and Meffe (1989) emphasized that mosquitofish most readily establish in disturbed habitats, but they did not quantify their contention. Yet, Gila topminnows seem to have survived throughout their natural range after the major disturbance (to the human eye) of regional arroyo cutting in the 1890s (Hastings 1959, 1963, Cooke and Reeves 1976) until mosquitofish appeared 30 yr later. Also, periodic flooding, often touted as a major negative disturbance, is tolerated by native topminnows but selects against mosquitofish (Meffe 1985, Minckley and Meffe 1987).

In Redrock Canyon (Table 1), an area of long-term coexistence (Rinne et al. 1980, Stefferud and Stefferud 1995, Weedman and Young 1997), both species persist in rock pools and other depressions (often spring-fed) within and adjacent to erosive, high-gradient channels. Gila topminnows are consistently more abundant for a few months after floods, until mosquitofish reinvade from livestock ponds upstream and rebound to dominance. Post-flood enhancement of Gila topminnow populations has been similarly documented in Sharp Spring (Meffe 1983a, 1985) and for related Yaqui topminnows in Black Draw, Arizona (Galat and Robertson 1992). If floods are frequent enough, they may thus provide a "hedge" against extinction of the native.

Coexistence also may be favored if habitat size and heterogeneity allow spatial segregation (Meffe 1985). This hypothesis is based mostly in theory and on long-term co-occurrences in the upper Santa Cruz River, Sonoita Creek, and Redrock Canyon. It also is possible, however, that the first 2 are occupied only sporadically, reinvaded after extirpation by fish from elsewhere (Minckley et al. 1977), and do not represent actual, long-term syntopy. Those in the mainstream Santa Cruz may be augmented or reestablished after extirpation from Sharp Spring and/or adjacent Heron Spring where Sharp Spring fish were introduced and established. Sonoita Creek also could receive migrants from Fresno Canyon and its tributary Coalmine Canyon. The "new" wastewater-inhabiting stock in the Santa Cruz River (in a reach mostly dry in the past and not then supporting any resident fishes; unpublished data) must have come from upstream in the Santa Cruz or Sonoita Creek, or both. It also is possible that unknown stocks are involved.

Table 1. General description and status of natural populations of Gila topminnow in the United States, based on Weedman and Young (1997) and original data; localities are indicated by numbers in Figures 1 and 3. The year in parentheses is when monitoring was last accomplished; statements of conservation status set in boldface type refer to that visit.

1. Sharp Spring (1995): low-volume flow through heavily vegetated channel, ~0.5 km long, isolated from Santa Cruz River except in flood; **topminnow greatly outnumbered by mosquitofish, most common in extreme springhead.**
2. Upper Santa Cruz River (1996, topminnow last taken 1993): heavily vegetated stream channel, commonly intermittent, with cut banks alternating with vegetated shorelines; subject to flood scour; topminnow occurs sporadically; consistently rare and often absent from collections (see also Minckley et al. 1977), **perhaps extirpated.**
3. Monkey Spring (1995): warm, constant-volume discharge changed little in past 30 yr (see, however, Minckley et al. 1991); **topminnow the only fish present in headspring and outlet, the former with a livestock exclosure.**
4. Cottonwood Spring (1996): warm, constant-volume discharge inside livestock exclosure; flows through short run into Sonoita Creek; **topminnow the only fish present in springhead and run, sometimes occurring with native longfin dace (*Agosia chrysogaster* Girard) in creek, which is intermittent or sometimes dry.**
5. Redrock Canyon, separated for sampling into Falls/Gate Spring (1995) and Cott Tank drainages (1996); typically intermittent channels subject to flooding, with small pools and streamside springs/seeps; **topminnow rare along with longfin dace at former, abundant with mosquitofish at latter; population sizes of both livebearers and presence of piscivorous centrarchid fishes variable.**
6. Sonoita Creek (1996): permanent reach in intermittent stream subject to flooding, bottoms sand/gravel, with some backwaters and pool-like habitats near obstructions; **topminnow abundant, occurring with native longfin dace, desert sucker (*Pantosteus clarki* [Baird and Girard]), introduced mosquitofish, and 1 or more species of introduced cyprinid, centrarchid, and ictalurid fishes.**
7. Fresno Canyon (1996): stream smaller but similar to 6, above; **topminnow present along with introduced centrarchids.**
8. Coalmine Canyon (1996): stream smaller but similar to 6, above; **topminnow abundant along with longfin dace and rare introduced centrarchid.**
9. Lower Santa Cruz River (1996): relatively swift channel over sand bottom; **topminnow present and common at 3 of 4 sites in a 5.0- to 6.0-km reach, occurring with longfin dace and desert sucker;** mosquitofish taken in 1994.
10. Ciénega Creek (1995): permanent stream similar to locale 6, above; **topminnow present along with longfin dace and Gila chub (*Gila intermedia* [Girard]).**
11. Bylas Springs (1997): 3 small springs (S-1, S-2, S-3), originally flowing through narrow, heavily shaded, vegetated channels into marsh or directly into Gila River; **S-3, from which all topminnows were extirpated, recently renovated, modified, and topminnow stock from S-1 (retained in an artificial refugium) reintroduced in 1998; S-2 renovated in 1996 (mosquitofish successfully removed), modified, and original topminnow successfully reestablished.**

Biological Factors in Habitat Use

Also related to water quality are springhead occurrence and persistence of topminnows along with apparent exclusion (despite apparently ready access) of mosquitofish. Western mosquitofish and the related *G. speciosa* penetrate only into the lowermost spring runs within their native ranges (Hubbs 1995), parts of which surround a number of other endemic gambusias restricted to springheads in Texas, New Mexico, and northern México. Except under human-altered conditions (Hubbs 1957, 1971), mosquitofish do not move upstream to replace these spring-specialized gambusias. Hubbs and Springer (1957) even hypothesized a scenario of origin in which invading mosquitofish stopped short of springheads, resulting in isolation of progenitors of the endemics. Based on today's examples (Marsh and Minckley 1990), topminnows share with these endemic gambusias an ability to live in springheads and the inability to cope with mosquitofish.

As fish habitat, springs have long presented a dilemma. Despite a significant number of western fishes depending for existence on springs or spring-fed environments (Meffe 1989), not many kinds consistently occupy the immediate areas in which subterranean waters rise to the surface. We rarely know why one succeeds in such places while another species fails (Courtenay and Meffe 1989, Hubbs 1995). A few springheads are simply too warm or present some other, insurmountable physiological challenge such as low dissolved oxygen (Sumner and Sargent 1940, Hubbs and Hettler 1964, Hubbs et al. 1967). Yet, most seem quite hospitable, at least to human senses. It seems

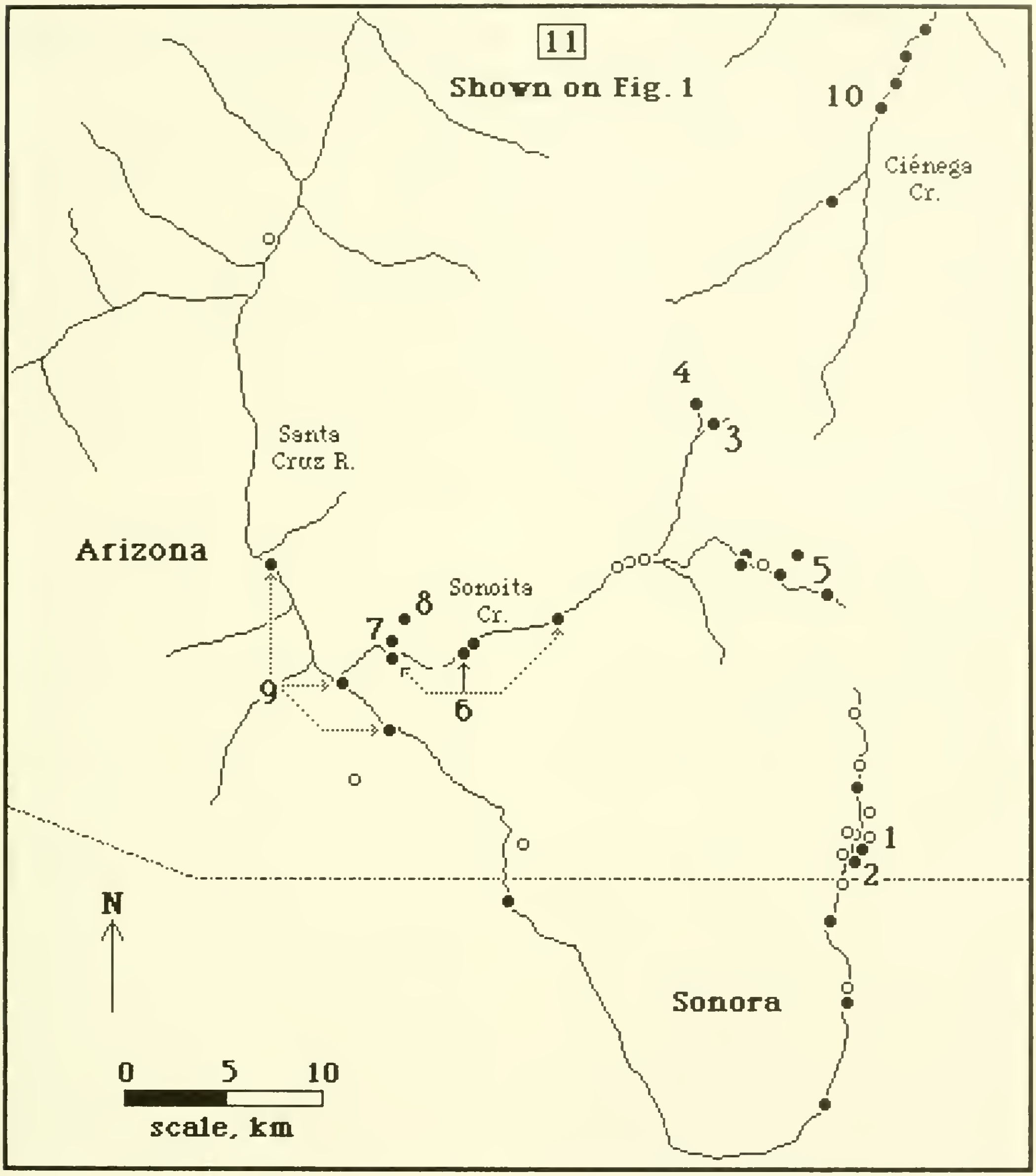

Fig. 3. Past (open circles) and present (dots, record sites 1987–1997) distribution of collection localities for Gila topminnows in the upper Santa Cruz River basin. Numbers are for present-day localities of natural (= wild) populations (see also locality 11 in Figure 1).

likely that springheads present one or more chronic extremes too severe over the long term for some species to succeed (e.g., constancy may exclude animals requiring thermal change for gonads to mature). Springheads most often are occupied by a single fish species, sometimes endemic, and often locked into the habitat by a specialization like stenothermy.

Some spring-inhabiting fishes may, in contrast, be equally capable of living elsewhere, often under apparently harsh conditions. Examples include pupfishes (genus *Cyprinodon*), some thriving equally as well in highly fluctuating habitats as in springs. Most of these taxa, despite their tolerances, avoid other fishes and tend to remain allotopic in particular habitats marked by constancy (as in springs) or severity (high temperatures, hypersalinity, etc.), excluding all but themselves. Gila topminnows in the Gila River basin may be one of the last group, living for millennia as part of a depauperate aquatic biota essentially free of piscivores or even species in similar habitats, which may be reflected in their present susceptibility to predation (Meffe 1983a, 1985). In rivers of México, Gila and Sonoran topminnows have dealt successfully over evolutionary time with larger fish faunas. Thus, their as-yet-unknown responses to mosquitofish (introduced in ~1978; Hendrickson et al. 1981) are important to document.

Mosquitofish seem more suited to habitats less constant than springs (see papers in Meffe and Snelson 1989) and survive under conditions of extreme variability, though not so severe as those tolerated by pupfishes. Unlike many springhead-inhabiting taxa, however, mosquitofish evolved and commonly occur where ubiquitous, predatory fishes are diverse and abundant. They also can spread quickly through artificial and natural habitats alike, so long as forces such as floods (Minckley and Meffe 1987) or environmental constancy do not interfere.

In light of all this, another plausible explanation for occasional topminnow-mosquitofish coexistence is that the native can recognize, occupy, and persist in springlike places within streams. Springs in stream bottoms are not exceptional, and extremely local conditions could give topminnows enhanced benefits (e.g., sufficiently deter mosquitofish success) for survival. Such refugia could exist where both fishes co-occur in the upper Santa Cruz River, flowing in a broad valley with a high water table and springs; Redrock Canyon, receiving groundwater in at least 6 places (Rinne et al. 1980, Stefferud and Stefferud 1995); and/or Sonoita Creek below Patagonia Lake (Fig. 3). In the last area the 2 fishes occupy borrow pits and channels downstream from an artificial reservoir. Permanency results from groundwater inflow (partially reservoir seepage) and enhanced stability below the dam. Floods are bypassed via a spillway (in part), and thermal variability is reduced by seepage, both simulating headspring conditions. As noted before, springs and seeps from banks and marshlands also are common along Ciénega Creek, which supports the largest existing topminnow population in the United States and where mosquitofish have not yet been detected.

An Unexplored Option

Another alternative perhaps pertinent to coexistence was examined by Hubbs (1991, 1992, 1996), who discovered that some western mosquitofish do not cannibalize their young, while others do. Non-cannibalistic individuals, if introduced and established in Arizona, might ignore young topminnows as well. Mosquitofish in Arizona almost certainly are of many different origins and times of stocking, and so benign stocks might be present, even though the single population tested (Hubbs 1992) was cannibalistic.

An Alternative Hypotheses

It seems more than coincidence that a large proportion of past and present topminnow localities are positioned at or near some form of groundwater inflow. I hypothesize that prolonged or extreme winter cold historically contributed and presently contributes to population extirpations, except in places where groundwater exchange or other factors ameliorate local water temperatures. Gila topminnow, like many other taxa with tropical and subtropical affinities, may be unable to survive prolonged winter cold. Coupled with other human-induced stresses, lack of cold resistance potentially leads to extirpation of northern, higher-altitude, and other unprotected stocks. As briefly reviewed above for Sonoran Desert plants, numerous examples of cold limitation are obvious in latitudinal and altitudinal distributional gradients, and fishes are no exception.

DISCUSSION AND SYNTHESIS

Most terrestrial organisms recognize few barriers to dispersal and redistribute readily after population reductions. Fishes, absolutely restricted to water in linear systems with varying connectedness, and especially so in arid lands, may require more time or special conditions to recolonize. Thus, in other than the few places with permanent, relatively warm water throughout their geographic range in the Gila River watershed, Gila topminnows in the past lived "from feast to famine," with highly variable population size and geographic range.

Historic conditions no longer exist and will likely not be reattained. The following interpretations of past conditions are integrated with today's realities of reduced water supplies, barriers to dispersal, mosquitofish, and other factors acting against long-term topminnow survival in nature.

An Ecological Scenario

The original, widespread distribution of the Gila topminnow in the Gila River basin (Fig. 1) must have depended on dispersal from secure refugia in times of abundant surface water, maximal habitat connectedness, and moderate winter temperatures. The fish is small and does not require high-volume habitats, deals readily with variations in chemical and physical environment, and has generalized food habits; few piscine predators were originally present. Its high reproductive potential with stored sperm and superfetation allowed 1 or a few females, each potentially inseminated by more than 1 male, to reliably establish more stocks with more genetic variability than possible by most other fishes. Rapid maturation of young assisted local stocks, perhaps the progeny from a single female, to expand rapidly up- and downstream. Fish dispersing to exploit food, space, or other resources in temporary habitats enjoyed greater reproductive success and accelerated the dispersal process despite greater individual risk incurred by leaving safer refugia. More sedentary fish provided insurance for individual and species survival by remaining in or near the most permanent oases.

Expanded populations then were destroyed, progressively due to extended drought or abruptly by sudden winter cold, again leaving isolated remnants. Magnitude of extirpation depended on severity of conditions. But by then the period of connectedness had allowed stocks to mix among refugia, ensuring maintenance of genetic diversity and reducing effects of bottlenecks accrued from earlier events. New individuals or their distant progeny also reattained some original refugia, mixing with progeny of individuals that stayed home. And, alternatively and in addition, other fish finding new groundwater-fed habitats survived there. Under natural conditions, one way or another, assurances existed that future offspring were available to disperse when conditions again were right.

Possible Substantiation

Significant genetic divergences among today's fragmented topminnow stocks (Monkey, Sharp, and Bylas springs, Ciénega Creek; Fig. 3), attributed mostly to differentiation in isolation by Parker et al. (1998a, 1998b), alternatively may reflect genetic variation derived from elsewhere and accumulated in refugia through repeated cycles of immigration. Thus, maintenance of diversity may be relatively high due to random immigration of different genotypes into each subpopulation, resulting over repeated cycles in an accumulated genetic variability (Birky et al. 1989). If this is correct, topminnows spreading from various refugia under pristine conditions mixed their genomes in "good" times. Differentiation among stocks arose through alleles accumulating from elsewhere and bottlenecks (Chakraborty and Nei 1977). In new and old refugia alike, divergence could be relatively high or low depending on source(s) and number(s) of founders. A few individuals could increase the level of apparent differentiation (Maruyama and Kimura 1980), and many or a few founders each from a number of sources could cause it to decrease (Slatkin 1977). A combination of these 2 processes, driven repeatedly by weather, resulted in today's apparent conditions. At a given moment in time, genetic or demographic equilibrium may seem minimal; averaged over a longer term, both likely exist.

In places like Monkey Spring, isolated by a substantial barrier (Minckley et al. 1991), unidirectional gene flow allowed differentiation in allotopy; Monkey Spring fish are genetically unique among 4 populations studied thus far (Parker et al. 1998a, 1998b). They average 0.62 private alleles per locus (sensu Slatkin 1985) for 5 polymorphic microsatellite loci compared with 0.14, 0.15, and 0.25 in 3 less isolated stocks (Bylas and Sharp springs, Ciénega Creek). Genes from Monkey Spring nonetheless passed downstream to be assimilated and transferred among other stocks, as indicated in part by the reciprocals (shared alleles) in the above data (0.86, 0.85, and 0.75 shared loci, respectively). More variation is expected in the refugia least isolated from up- or downstream habitats into which dispersal occurs and from which fish potentially return.

This might be tested by examining existing populations throughout Sonoita Creek and Santa Cruz River (Campoy-F. 1996, Weedman and Young 1997). I predict they are genetically similar to existing stocks in known refugia. And if not, I can always rationalize failure of the prediction by advocating extinction (or presence) of unknown stocks. Such a situation may be analogous to that of razorback sucker, *Xyrauchen texanus* (Abbott), in the Colorado River basin, where highest genetic variability is concentrated downstream, again concordant with greatest population stability, and has apparently not yet redistributed upstream following far colder conditions of the last period of glaciation (Dowling et al. 1996).

In conclusion, patterns of expansion and contraction of geographic range through linear stream habitats are common for aquatic organisms during wet and dry seasons and in wet versus dry years. These patterns may be extended to far longer time scales for species such as topminnows and desert pupfish (Dunham and Minckley 1998) under arid land conditions, or native trouts (Rinne and Minckley 1985), the last isolated as relicts in headwaters on cool regional highlands by the hot, dry surroundings of today. If a refuge is sufficiently reliable to protect it (from either a cold desert night or from glacial or interglacial epochs), a lineage may survive to provide individuals potentially available to disperse and breed with individuals from other refugia, repopulating whole drainages when conditions allow. It must have happened repeatedly through climatic cycles at both geologic and ecologic time scales. If not, the available alternatives were to evolve in isolation into a new form(s) or disappear.

APPLICATIONS TO MANAGEMENT

If this scenario of dispersal →extirpation →redispersal →etc. approaches reality, human intervention has already been so disruptive that it may not be relevant to the modern day. In translocation-site decisions, however, considering thermal relations might result in greater success, and other interpretations from the anecdotal record may also be significant in furthering species maintenance.

I question a recommendation by Simons et al. (1989) to create what has come to be called management units, to preserve "at least one representative lineage from each of the 4 geographic areas in Arizona" (Monkey Spring, Sharp Spring, Bylas Springs, and Ciénega Creek). Moritz (1994) defined management units genetically as "diverged in allele frequency and significant for conservation in that they represent populations connected by such low levels of gene flow that they are functionally independent." This may be true if today's human-created barriers to natural dispersal are considered significant, but it was certainly not the case under historical conditions when topminnows and many other western American stream fishes evolved and lived. Further, perhaps excluding the differentiated Monkey Spring population (Parker et al. 1998a, 1998b), the "evolutionary significant unit" (Waples 1995) for topminnows in the Gila River system is the whole population (or metapopulation), not its component parts, and it should be managed accordingly. For further discussion, alternative views, and citations relevant to conservation genetics of Gila topminnow, see Cardwell et al. (1998), Hedrick and Parker (1998), and Parker et al. (1998a, 1998b).

The following summarizes the 4 major disruptions that must be overcome to prevent extinction of the Gila topminnow, each followed by brief management recommendations that, when combined, could result in recovery of the species:

(1) Present-day and potential future connectedness are greatly reduced or nonexistent, not only during drought but also in wetter times due to diversion and drying of whole rivers (e.g., lower parts of the Gila, Santa Cruz, and Salt rivers mainstems) and many lesser watercourses as well. Topminnow can no longer swim from "point A to point B." Individuals therefore must be translocated directly by managers.

(2) Most refuge has been destroyed (through groundwater removal) or rendered inaccessible (through disrupted connections and see below) to recolonization by dispersing topminnows. Existing natural refugia (both natural and reestablished) must therefore be protected at all costs and remaining stocks kept at appropriate size and genetic quality. Artificial refugia and translocated populations also must be established and maintained, likely in perpetuity.

(3) Ecological information indicates a pattern of dispersal from refuge in "good" times and retreat into refuge in "bad"

times. This pattern must be re-created periodically through direct transfers, which further involve acceptance of local extirpation countered by active and continued movement of individuals from less-than-permanent places back to reliable refugia by managers, to mimic the species' natural ecology. Monkey Spring fish should be maintained without influx of genes from other populations, but allowed to contribute to other stocks.

(4) Even if refugia remain present or are established and connectedness can in some way be reestablished, intervening habitats now harbor mosquitofish and other predators that interdict and devour dispersing topminnows and their progeny. This requires elimination, exclusion, or effective management against offending species. They must be eliminated from refugia and their nearby populations controlled to minimize the probability and frequency of invasion.

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LIMITATIONS ON CANADA GOOSE PRODUCTION AT FISH SPRINGS NATIONAL WILDLIFE REFUGE

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ABSTRACT.—At Fish Springs National Wildlife Refuge, only 18 to 34 Canada Goose goslings were fledged per year from 1989 to 1993. In addition to the number of breeding pairs, a wide variety of variables can influence goose production, including clutch size, and nest, egg, and fledging success. We examined these variables at Fish Springs in 1996 and 1997 by finding and monitoring nests, and then following broods. We found that despite a limited number of breeding pairs on the refuge, production was further limited by poor ground nest success and low fledging success. Only 51.2% (n = 22) of ground nests produced hatchlings vs. 86.4% (n = 19) of platform nests. Of all eggs that hatched, 36.8% (n = 57) fledged successfully. Predation and human disturbance are discussed as major factors contributing to mortality.

Key words: Branta canadensis, *Canada Geese, Fish Springs National Wildlife Refuge, fledging success, gosling mortality, ground nest success, salinity, Utah.*

Reproductive success in Canada Geese (*Branta canadensis*) is determined by a number of variables. Population size and age structure determine the number of potential breeders. Most female geese breed and pair in their 3rd or 4th year (Bellrose 1980). However, not all paired geese become territorial. Of those that do defend a territory, not all will initiate nesting. Ball et al. (1981) and Hanson and Eberhardt (1971) estimated that about 20% of territorial pairs do not nest. The number of potential territories can be a limiting factor in nesting; however, higher geese densities may result in increased abandonment of nests due to harassment of the nesting female (Ewaschuk and Boag 1972).

Once nesting is underway, important variables contributing to recruitment are clutch size, nest success, egg success, and survival of young birds to fledging. Younger and less experienced geese lay smaller clutches (Brakhage 1965, Finney and Cooke 1978, Lessells 1982, Rockwell et al. 1983) and raise fewer goslings to wing (Brakhage 1965, Finney and Cooke 1978, Raveling 1981). Adult body size appears to be loosely related to clutch size because nutrient reserves influence clutch size (Ankney and MacInnes 1978, Raveling 1979, Lessells 1982; but see Davies et al. 1988).

Nest success may depend upon location. Elevated platforms experience less predation than ground nests (Krohn and Bizeau 1980), and island ground nests are depredated less often than mainland ground nests when terrestrial predators are present (Klopman 1958, Vermeer 1970, Johnson and Shaffer 1990). A territory with poor forage may cause a female to spend more time off the nest feeding, leaving the nest vulnerable to predation. Conversely, Ankney and MacInnes (1978) found incubating female Snow Geese dead on the nest, apparently from starvation. Flooding can be a problem during the nesting season (Bellrose 1980). An estimated 85% of monitored nests were flooded in a section of marsh in northern Utah in 1997 due to snowmelt and extremely high water levels in the river feeding the marsh (D. Stolley personal observation). Nest success also is influenced by age and experience of the breeding pair (Raveling 1981). Older, more experienced females generally have more body reserves (Aldrich and Raveling 1983), due either to more efficient foraging or to the ability of the male to provide protection from conspecific harassment, allowing the female more feeding time (Raveling 1981). Heavier females are more attentive to their nests (Aldrich and Raveling 1983), leading to less likelihood of predation. Experienced ganders are more successful at keeping other geese away from the incubating female. Abandonment may be caused by harassment of the nesting female by other geese (Ewaschuk and Boag 1972, Bellrose 1980, Raveling 1981), malnutrition (Harvey 1971, Ankney and MacInnes 1978), or human disturbance (MacInnes and Misra 1972, Bellrose 1980).

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Egg success is important in determining number of offspring. Often, eggs in a nest do not hatch and are either infertile or contain dead embryos. Occasionally, a female will lay eggs after full incubation has begun; thus, in the same nest normally developing eggs may not hatch synchronously. Females may incubate these eggs longer and successfully hatch them but often may abandon them as the earlier hatched goslings are led to the brood-rearing area. Contaminants can lower egg viability or produce deformed goslings that do not hatch or are incapable of surviving in the wild.

Similarly, many variables can affect fledging success in geese. Fledging success is measured as the percentage of hatched goslings that survive to reach flight stage, about 70 d (Yocom and Harris 1965, Eberhardt 1987). Most Canada Goose gosling mortality occurs in the first 10–14 d after hatching (Geis 1956, Steel et al. 1957, Martin 1963, Dey 1964, Mickelson 1973, Krohn and Bizeau 1980, Ball et al. 1981, Eberhardt et al. 1989, Sargeant and Raveling 1992). Predation is an important cause of mortality in goslings (Geis 1956, Brakhage 1965, Sherwood 1966, Mickelson 1973, Wang 1982, Sedinger 1992). Likewise, disease can have catastrophic effects on a population. Sherwood (1966) documented gosling survival of only 16% after a 1964 outbreak of a *Leucocytozoon* blood parasite in Michigan. He also noted that when goslings were very young, human disturbance often resulted in abandonment of slower or separated goslings. Because nutrition is an important factor in growth and development of all young birds, inadequate nutrition can lead directly to mortality due to starvation or lack of essential minerals. It also can result in weak or small birds that more easily succumb to predation, exposure, or disease, or birds that are unable to keep up with their siblings. The quality of parental care affects fledging success in geese. Inexperienced or inattentive parents may not lead goslings to good grazing areas, guard well against possible predators, or react protectively against danger (Raveling 1981).

In the early 1960s Canada Geese were established at Fish Springs National Wildlife Refuge (NWR) in the west desert of Utah through release of captive birds and arrival of wild birds. From 1965 to 1969 Canada Goose numbers gradually increased, as did gosling production. The highest estimates of gosling production were made in the mid-1970s, but differences in census methods make these estimates suspect. From 1983 to 1987 the number of nesting pairs present on the refuge during the breeding season declined. From 1989 to 1993 nesting pair numbers ranged between 18 and 22. Gosling production during this same time was between 18 and 34 birds. We conducted field research March–July 1996 and 1997 to determine factors limiting gosling production at Fish Springs NWR. To do this, we quantified the number of territorial and breeding pairs and compared the numbers with historical data; we measured clutch size and documented nest and egg success; and we quantified fledging success.

STUDY AREA

Fish Springs NWR is located at the southwest edge of the Great Salt Lake Desert in Juab County, Utah. As ancient Lake Bonneville lake bottom, the refuge is very flat and the soil is saline and alkaline. Five major and several minor thermal springs arise from a fault line running parallel to the east side of the Fish Springs mountain range and feed the refuge's 8900-acre marsh. Fish Springs NWR was established in 1959. Impoundments and other marshland development to provide habitat for waterfowl were completed in 1964. It is not known definitely whether Canada Geese nested in this area prior to establishment of the refuge (Annual Report, Fish Springs NWR, 1982; J. Banta, Fish Springs NWR, personal communication); however, they were not nesting in the refuge area in the late 1950s.

After the refuge was established, 9 large, shallow pools, impounded by dikes and fed from the springs through canals, were created, enlarging and modifying the natural marsh. Much of the more southern impoundment area, viz., Avocet, Mallard, Curlew, Egret, and Shoveler, was original slough and contains numerous islands and peninsulas, as well as typical emergent marsh vegetation, e.g., Olney's three-square bulrush (*Scirpus americanus*), cattail (*Typha domingensis*), hardstem bulrush (*S. acutus*), alkali bulrush (*S. maritimus*), wirerush (*Juncus arcticus*), and saltgrass (*Distichlis spicata*). Abundant mats of submergent vegetation, primarily wigeongrass (*Ruppia maritima*), muskgrass (*Chara* spp.), spiny, or pond, naiad (*Najas marina*), and coontail (*Ceratophyllum demersum*) grow in the springs, canals, and pools. Additionally, the native *Phragmites australis* has expanded into much of the marsh. Northern impoundments, viz., Ibis, Pintail, Harrison, and Gadwall, were constructed on the northern edge of original wetlands and contain little of the original marsh structure. Most water feeding these pools comes from more southern pools. These impoundments become dry or reduced during summer because spring input volume cannot match evaporation rates. Vegetation bordering these impoundments is characterized by saltgrass (*Distichlis spicata*), pickleweed (*Allenrolfea occidentalis*), and annual samphire (*Salicornia europaea*). The impoundments contain little emergent or submergent vegetation.

METHODS

Determination of the Number of Territorial and Breeding Pairs

To quantify number of territorial pairs, we conducted daily to weekly pair counts and daily to twice weekly observations of territorial and nesting behavior 22 March–5 May 1996, and 21 March–11 May 1997. We drove slowly along the dikes surrounding every impoundment and made observations from our vehicles using spotting scopes. Pairs, singles (assumed to be males with a mate on a nest), aggressive behavior, and nesting behavior were recorded and location of geese marked on a map. To determine if territorial pairs were breeding, we located nests. We observed artificial nesting platforms for signs of use and checked them several times during the season. We located ground nests with a variety of techniques. The vast majority were found from an air boat. Every impoundment was completely traversed by air boat at least once, and many twice, during the early part of nesting seasons. During our daily observations we scanned for signs of incubating females and small pieces of down in the vegetation, indicating a possible nest. We also looked for single ganders that might be guarding an incubating female, particularly in areas that previously had a pair evident. We found several nests and general nesting areas this way. We also traversed areas of the marsh by foot and inflatable kayak. We examined historical data on number of pairs by searching file archives at Fish Springs NWR headquarters for relevant information. We read study reports for 1983 and 1989–1994 as well as excerpts from all annual reports. We also examined archived pair count data. Unless noted otherwise, annual and goose study reports cited in the text are from Fish Springs NWR.

Pre-hatching

To quantify clutch size, nest success, and egg success, we observed nests from a distance, checking them by foot if we suspected that incubation was underway or that the nest had been abandoned. In 1996 we avoided checking either platforms or ground nests if we suspected the female was still laying. We did not check ground nests in 1997 when the female was laying. All eggs were counted, numbered, and candled to ascertain viability and approximate stage of development. We monitored status (i.e., incubating, pipping, abandoned, depredated) of all nests until broods had hatched and left the nest. We then returned to the nest to count and collect unhatched eggs for analysis. To determine number of infertile eggs and those with dead or decomposed embryos, we opened unhatched eggs.

Post-hatching

To quantify fledging success and determine whether mortality was related to location, we monitored gosling numbers and location by observing neck-banded, radio-collared, and unmarked adults. Many researchers use survival to a certain age (i.e., 4–6 wk, 8 wk, banding) as a surrogate for survival to fledging; we used survival to banding (≈8 wk after hatching) to estimate fledging success.

In 1996 we trapped nesting females and collared them with yellow plastic neck bands inscribed with individual alpha-numeric codes. We collared additional adults and some goslings during the period when adults were flightless. In 1997 we took various measurements of each female, including body mass, and wing, culmen, tail, and total body lengths, and installed alpha-numeric color-coded collars equipped with radio transmitters. Our trapping activities were concentrated on nests where neither parent was collared. Because females are less likely to abandon their nests when eggs are pipping, we trapped at this time (Eberhardt et al. 1986). We approached the nest, flushed the female, and set up a bownet trap modified from a design by Shor (1990) to include a remote-control trigger. We returned after 2–4 h to spring the trap from a distance of 50–150 m. Three of 5 trapped females abandoned their nests in 1996. In 1997, to prevent nest abandonment, we utilized an injectable anesthesia, Propofol (Rapinovet; Mallinckrodt Veterinary, Inc.); only 1 of 8 females abandoned her nest.

After broods left the nest, we returned to ascertain the number hatched. Unhatched eggs were collected and examined. We attempted to locate all broods every day for the first 15 d following hatching, and then every other day. Broods were located by telemetry or observation, and location and number of goslings noted. Some broods moved from one pool to another. Some deaths occurred during an interval when a brood was not located; these were recorded as unknown deaths. We counted deaths occurring during an overland move of more than 200 m as deaths in transit. Overland moves of <200 m were not considered in transit.

RESULTS

Numbers of Pairs

Prior to 1978 no pair counts were made at the refuge. From 1978 to 1987 pair counts during the breeding season ranged from 58 to 77. No distinction between total pairs and territorial or nesting pairs was made. During the 1988 breeding season, 25–40 pairs were present. From 1989 to 1993 numbers of nesting pairs ranged from 18 to 22. No pairs counts were done in 1994 or 1995. In 1996 we made 24 refuge-wide goose pair counts between 22 March and 5 May. Approximately 35 pairs became territorial; 26 (74%) of them nested. In 1997 we made 19 counts from 21 March to 11 May; our pair counts ranged from 31 to 52 and averaged 41. Observations and territory mapping yielded about 43 territorial pairs. Of these, approximately 34 (79%) nested, producing 39 known nests. Thus, 5 pairs (15%) of 34 were responsible for 2 nests apiece. Our observations suggested that all renests were the result of continued laying. No 1st or 2nd nests of the same pair contained more than 3 eggs or eggshell fragments of more than 3 eggs.

Pre-hatching

CLUTCH SIZE.—We calculated clutch size for all complete nests after full incubation had started. In 1996 mean clutch size for artificial nesting platforms was 5.33 ± 0.71; for ground nests it was 4.42 ± 1.51 (range 2–6). When suspected renests were added to the first clutch, mean clutch size for ground nests was 5.30 ± 0.82. In 1997 mean clutch size for artificial nesting platforms (n = 10) was 5.70 ± 1.64. One nest contained 10 eggs, 5 of which were infertile; disregarding these, mean clutch size was 5.20 ± 0.63. Mean clutch size for ground nests (n = 19) was 4.68 ± 1.42. Including renests, mean clutch size for ground nests (n = 17) was 5.29 ± 0.77 (range 1–10). In 1996 and 1997 overall mean clutch size for *successful* nests (i.e., ≥1 eggs hatched) was 5.3 ± and 5.3 ±, respectively.

NEST SUCCESS.—We located 28 nests in 1996. Geese nested on 10 (58%) of 17 available artificial nesting platforms. We found 18 ground nests, 2 of which were abandoned due to human disturbance at the nest during laying. Pairs in the disturbed nests renested; these were not used in calculating nest success. However, for this calculation we considered as successful those nests that contained pipping eggs but were subsequently abandoned due to our trapping efforts. Overall nest success (i.e., ≥1 eggs hatched) was 69%; 18 of 26 nests were successful. Nine (90%) of 10 platform nests were successful. Nine (56%) of 16 ground nests were successful. In 1997 we located 36 nests. Twelve (70.6%) of 17 artificial platforms were utilized, 10 of which (83.3%) were successful. Ten (41.6%) of 24 ground nests were successful. Three ground nests were assumed to exist because of the appearance of broods otherwise unaccounted for. Thus, ground nest success may have been as high as 48.1% (13 of 27 successful), and overall nest success 59.0% (23 of 39 successful). Over 2 yr goslings were produced in 64 nests. Even though ground nests produced more goslings (n = 22) than platform nests (n = 19), ground nests were less successful (51.2%, n = 43) than platform nests (86.4%, n = 22).

FATE OF UNSUCCESSFUL NESTS.—Of 28 nests found in 1996, 5 were found depredated. The

TABLE 1. Egg success from nests that hatched at least 1 Canada Goose egg at Fish Springs NWR, Juab County, Utah.

Year	Number nests	Total number eggs	Average clutch size	Number infertile eggs	Number rotten eggs	Number normal[a] eggs	Total hatched (egg success)[b]	Average hatch per nest
1996	14	75	5.4	2 (2.7%)	1 (1.3%)	2 (2.7%)	70 (93.3%)	5.0
1997	20	106	5.3	7 (6.6%)[c]	3 (2.8%)	11 (10.4%)[d]	85 (80.2%)	4.25

[a] We use "normal" to designate unhatched eggs with normal embryos that did not begin pipping.

[b] Pipping eggs from nests that were abandoned due to trapping efforts and subsequently did not hatch are counted as hatched for this calculation.

[c] Five infertile eggs were from 1 nest that also contained 5 fertile eggs.

[d] Our activities at the nest may have caused broods to leave earlier than they would have normally, abandoning unhatched eggs, as many as 7 eggs may have been affected by this.

following year 13 of 36 nests were depredated, 8 by avian predators including ravens (*Corvus corax*). At 2 nests we also found owl pellets. Three nests appeared depredated by coyote (*Canis latrans*), and 3 others were destroyed by an unknown predator. Of 13 depredated nests we do not know if abandonment came before or after depredation. However, one may have been abandoned due to harassment at the nest, first by a Golden Eagle (*Aquila chrysaetos*) and later by our checking the nest. Another nest appeared to have been abandoned due to harassment by conspecifics; we observed aggressive interactions between geese in the nest vicinity both before and after the egg loss. In 1997, 2 nests were abandoned, apparently due to our visiting the nest.

EGG SUCCESS.—Eighteen nests were successful in 1996. We used 14 nests with complete histories to compute egg success (Table 1). Seventy-five eggs were used in the calculations. Overall, 5 (6.7%) did not hatch, for an egg success rate of 93.3%: 2 (2.7%) were infertile, 1 (1.3%) had decomposed, and 2 (2.7%) contained normal embryos that had not hatched. We calculated egg success for 20 of 23 successful nests in 1997 (Table 1). Of 106 eggs laid, 21 (19.8%) did not hatch: 7 (6.6%) of the 106 were infertile, 3 (2.8%) were decomposed, and 11 (10.4%) contained developed embryos that had not pipped. Over the 2-yr-study, 26 (14.4%) did not hatch. In both years we examined all eggs that did not hatch and found no evidence of physical deformities. One egg contained twins; they were normal but several days behind their nestmates in development. Mean egg success for the 2 yr was 85.6% ($n = 155$).

Fledging Success

In 1996, 70 eggs hatched and 14 goslings (20%) survived to fledging. In 1997, 85 eggs hatched from 20 nests; 43 goslings (50.6%) survived to fledging. Three nests containing a total of 13 eggs were counted as "successful" for nesting success estimation; however, they were abandoned as pipping eggs or hatchlings due to trapping efforts, and so cannot be used in fledging success estimation. Another 3 goslings from successful nests died immediately after hatching due to trapping efforts; they were not included in the count of 85 hatched eggs. In 1997, 37 goslings hatched in platform nests; 18 (48.6%) fledged. Forty-six goslings hatched in ground nests; 25 (54.4%) fledged. Platform and ground nest fledging success was not significantly different ($\chi^2 = 0.20$, $P = 0.66$).

EFFECT OF LOCATION.—We examined number of gosling deaths per use-day (DPUD) on all brood-rearing impoundments for 17 broods (Table 2). Seven broods were with radio-collared females, 5 were with 1 or both parents that wore neck bands, and in 5 broods neither adult was collared. We identified these broods by age of goslings and location. The 17 broods hatched 75 goslings. We counted hatching day as day 0. By the end of day 1, all broods had left the nest. By day 15 following hatching, 42 goslings (56%) were still alive; 33 (44%) had died. The mean number of DPUDs during this period was 0.0435. Four locations had below-average DPUDs: Harrison, Ibis/S. Gadwall, Pintail, and Shoveler. Two locations, Mallard and Green Pond, had DPUD numbers that ranged from 0 to above average. Three locations (Egret, Curlew, and N. Gadwall) and birds "in transit" had above-average DPUDs.

BREEDING EXPERIENCE.—We collared 5 females in 1996, all of which incubated their clutches to pipping, returned to the same general nesting vicinities with mates in 1997, and became territorial. At least 4 of them nested,

TABLE 2. Number of Canada Goose gosling deaths per use-day through day 15 after hatching at Fish Springs NWR, Juab County, Utah, 1997.

Location	No. of use-days[a]	No. of deaths[b]	Deaths per use-day
Ibis/S. Gadwall	143–144	2	0.014
Harrison	184–187	2–3	0.011–0.016
Pintail	162–163	3	0.018
Shoveler	43	1	0.023
Unknown	69–95	3–4	0.032–0.058
Green Pond	10–12	0–1	0–0.100
Egret	75–104	10–12	0.096–0.160
Curlew	6	1	0.167
N. Gadwall	12	3	0.250
In transit	17–19	1–8	0.053–0.471
Mallard	6	0–3	0–0.500
TOTALS	727–791	33[c]	n.a.
AVERAGE	n.a.	n.a.	0.042–0.045

[a] Ranges in number of use-days resulted from days when we located a brood but were unable to make an exact count of goslings.
[b] Ranges in number of deaths at a specific location resulted from our pinpointing mortality to 1 of 2 locations rather than to the exact location.
[c] Exact number of mortalities.

and 1 successfully hatched a brood and raised 2 goslings to fledging. Another 5 pairs may have been returning pairs; they nested early and utilized artificial nesting platforms that were used the previous year. We suspect another 7–8 pairs had prior breeding experience at Fish Springs due to a combination of clues, including nest placement and behavior. One collared male and a mate were present on the refuge in 1996 but did not breed; in 1997 they successfully fledged 3 goslings.

DISCUSSION

Nesting Success

Our results show that low recruitment rates of geese at Fish Springs National Wildlife Refuge are in part a result of low nesting success, particularly of ground nests. Although ground nests fledged more goslings, nests on platforms had greater nesting success. There are several possible explanations for this. First, female geese leave the nest periodically and are usually accompanied by the gander (Bellrose 1980), leaving the nest vulnerable to predation. Avian and mammalian predators are common on the refuge, especially Common Ravens and coyotes, which are ubiquitous. The elevated platform nest is more visible at a distance to the gander than a ground nest and predation attempts more easily detected. Second, it appears that experienced pairs are using platforms. Successful platform nests are initiated earlier than ground nests. We noted that birds we marked in 1996 returned earlier to the refuge in 1997 than most unmarked birds. More experienced, older breeders often begin incubation with more body reserves and spend less time off the nest feeding. First-time breeders develop and strengthen their pair bond on wintering grounds, thus often arriving later on breeding grounds. Once on the breeding ground, naive birds often find the best territories occupied. Additionally, Aldrich and Raveling (1983) showed that 1st-time breeders lay smaller clutches than experienced breeders. However, our analysis of clutch size, if renesting is taken into account, shows remarkably similar clutch sizes for platform and ground nests in both 1996 and 1997. In addition to being vulnerable to avian predators, ground nests are at risk from mammalian predators. The most common mammalian predator at the refuge is the coyote; however, red foxes (*Vulpes fulva*) and striped skunks (*Mephistis mephistis*) are also present.

Females on ground nests appear to react more strongly to disturbance, often leading to nest abandonment. In 1996 and 1997 we unintentionally flushed laying females from their ground nests of 1–2 eggs while conducting nest searches. In all cases (2 each year), females abandoned the nests. In 1996 we checked 4 platform nests before the clutch was completed. In no case did we flush the female from the nest, although in at least 2 cases the pair was in the vicinity. In 1997 we checked 4 platform nests with incomplete clutches, flushing females from 3 of these nests. There were 3 eggs as well as down feathers in each nest, indicating initiation of incubation (Cooper 1978). No females abandoned platform nests during laying because of observer visitation.

The general wariness of nesting females at Fish Springs compared with other populations may have significance. In 1996, 4 of 6 collared females abandoned their nests because of activities related to our capture attempts. Four females did not return to the nest until the trap was removed. Other researchers who have trapped nesting female geese found this unusual (J. Sedinger, University of Alaska, personal communication; T. Aldrich, Utah State Division of Wildlife Resources, personal communication). Eberhardt (1987) trapped 41 nesting females for radio-tagging. Of these, only 7 (17%) abandoned. Abandonment late in incubation, or while eggs are hatching, suggests that female geese on the nest may be responding to proximate conditions (i.e., low body reserves). Fish Springs NWR nesting females did weigh less than Cutler marsh nesting females.

Low Fledging Success

We found that fledging success at Fish Springs was uncharacteristically low for this species and that most mortalities occurred in the first 15 d following hatching. Geis (1956) found significant mortality during the first few days following hatch as broods trekked overland from nesting areas to brood-rearing areas. She attributed most mortalities to predation. This appears to be what happened to the goslings disappearing in transit at Fish Springs. We surmised by the timid behavior of nesting geese that defense against mammalian predators was either nonexistent or ineffectual. We observed that smaller goslings often were unable to keep up with the rest of the brood during trips through dense saltgrass or harsh upland desert. Wary parents often appeared to abandon slower young in favor of getting the others to safety as quickly as possible, suggesting that predation remains a significant selection pressure. During both 1996 and 1997, when we approached slowly in the truck, adults and young often would run into the upland desert away from the safety of water. We examined the area and found coyote tracks interspersed with goose tracks, as well as a coyote path, along a low (4-m-high) ridge that paralleled the dike and grazing area. In 1989 high gosling loss was reported in this area, attributed to easy access by coyotes (J. Engler, Goose Production, Fish Springs NWR, 1989). Additionally, in 1997 water levels were low enough to allow easy access by mammals to the islands and peninsulas within the pool. In 1996 a juvenile coyote with a dead adult goose in its mouth was observed on Pintail impoundment (K. Jenkins, Fish Springs NWR, personal communication). We also saw coyotes with pups apparently stalking geese.

Even though ground nests produced a few more goslings (22 vs. 19) than platform nests, ground nests were only about half as successful (51.2% vs. 86.4%). Additionally, broods reared on northern impoundments fared better than those on more southern areas. If localized numbers are below carrying capacity, it would seem that increasing the number of platforms available for nesting in northern impoundments may improve gosling production and fledging success.

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CHARACTERISTICS OF NATAL AND NON-NATAL KIT FOX DENS IN THE NORTHERN CHIHUAHUAN DESERT

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ABSTRACT.—We studied kit fox den characteristics on the northern McGregor Range of Fort Bliss Military Reservation, New Mexico, during 1994 and 1995. Twenty radio-collared kit foxes used 132 different dens, including 16 natal dens. Kit fox dens were located primarily in creosote-dominated habitat found in relatively flat, well-drained terrain. Natal dens were virtually indistinguishable from non-natal dens; however, natal den entrances were taller than non-natal den entrances. Entrances found at all dens were oriented more frequently toward the northwest and southeast. Kit foxes used more new dens during the breeding (January–February) and pup-rearing season (May–July) than during gestation.

Key words: Vulpes macrotis neomexicana, *kit fox, dens, habitat use, Chihuahuan Desert, soils, GIS.*

Ecology of the desert kit fox (*Vulpes macrotis neomexicanus*) in the northern Chihuahuan Desert has not been previously studied. The region includes southeastern New Mexico and southwestern Texas and is recognized by some biologists as a zone of sympatry between the kit fox and swift fox (*V. velox velox*). Some question remains as to which species inhabits this area (Rohwer and Kilgore 1973, Thornton and Creel 1975, Dragoo et al. 1990, Mercure et al. 1993). The U.S. Fish and Wildlife Service (FWS) has concluded that the swift fox is declining throughout its range and determined its listing "warranted but precluded" due to other higher priority species (U.S. Federal Register 1995). It is now listed as a species of concern. Because the kit fox is closely related to the swift fox and appears to have similar behaviors, baseline ecological data for kit fox may contribute to swift fox conservation efforts.

Previous studies on the effects of military activities on San Joaquin kit foxes (*V. m. mutica*) in California demonstrated few direct adverse impacts (Berry et al. 1992, Reese et al. 1992). Controlled public access including hunting and trapping, restricted vehicle traffic, and limited land development on several western military reservations may preserve suitable habitat necessary to sustain fox populations. Although authorized military activities such as missile firings, vehicle traffic, and field exercises may negatively impact some areas suitable for kit fox dens, such disturbance may positively alter vegetation important to prey populations. The primary concern on military lands, however, is destruction of suitable denning habitat by vehicles or construction.

Kit and swift foxes use underground dens for escape cover, protection from environmental conditions, and raising pups (Seton 1925). These foxes are 2 of the only canids to use dens year-round, and they typically use a subset as natal dens in which to raise pups (Morrell 1972). Egoscue (1975) suggested kit fox populations may be limited by available denning habitat. While this has not been definitively confirmed, the kit fox's strong dependence on den sites throughout the year is critical to its survival. We undertook our study to further understand kit fox denning behavior and to describe characteristics of natal dens, non-natal dens, and surrounding denning habitat on the northern McGregor Range of Fort Bliss Military Reservation, New Mexico. Recognition of differences in den traits and denning habitat may assist the military in land-use decisions.

STUDY AREA AND METHODS

Our study area encompasses approximately 53 km^2 in the northern portion of McGregor Range on Fort Bliss Military Reservation in south central New Mexico. Fort Bliss lies in the Tularosa Basin surrounded by the San Andres, Franklin, and Organ Mountains to the

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west, Otero Mesa and Hueco Mountains to the east, and Sacramento Mountains to the north. McGregor Range includes 288 km^2 of transition zone from the northern Chihuahuan Desert to the Sacramento Mountains. Elevation ranges from 900 to 1800 m. The area is arid to semiarid with variable precipitation of 8–25 cm per year (Gile and Grossman 1979). Vegetation consists of creosote (*Larrea tridentata*) and tarbush (*Flourensia cernua*) flats, grasslands predominantly characterized by burrow grass (*Scleropogon brevifolius*) interspersed with cactus (*Opuntia* spp.) and yucca (*Yucca* spp.), mesquite (*Prosopis glandulosa*) dunes, and saltbush (*Atriplex canescence*) dunes.

Military activities on McGregor Range include the firing of 7.62-mm coax machine guns, 25-mm Bradley fighting vehicles, Stinger and Avenger missiles, and HAWK and Patriot missiles. These munitions are launched from stationary firing positions into designated impact areas on north McGregor Range. Greatest military use occurs annually during 3 wk in May and June. Primary activities during this period include missile firings and field training. Vehicles, which range from 4-person Jeeps to 28-ton Patriot launchers, utilize only improved, designated roads. Approximately 3500 personnel are involved in off-road field training exercises primarily on Otero Mesa. The range is also used September through December for firing missiles into designated impact areas.

Kit foxes were live-trapped using single-gate, wire-box traps and fitted with radio collars during late January through early June 1994, and late January through February 1995 (Zoellick and Smith 1986, White et al. 1991). Traps were baited and opened for 4 nights. Foxes were handled without using immobilization drugs when possible. When immobilization became necessary, a 5:1 mixture of ketamine hydrochloride (Ketaset, 4.0 mg/kg) and acepromazine maleate (Promace, 0.25 mg/kg) was administered intramuscularly. All foxes were fitted with numbered ear tags. Adults were fitted with a 70-g radio collar equipped with an activity sensor and released at the trap site.

We identified known kit fox dens by tracking radio-collared individuals to dens 3–6 times per week 31 January–14 July 1994 and 1995. The number of dens used by foxes was determined for each of 3 seasons: breeding (31 January–28 February), gestation (1 March–30 April), and pup-rearing (1 May–14 July). Weekly den use was standardized using length of time in each breeding season (breeding 2.9 wk, gestation 8.7 wk, pup-rearing 10.7 wk). Seasonal descriptions of den use were based on observations of resident kit fox behavior.

We used 2 methods to analyze den use. First, we examined the rate of den site change by comparing average number of dens used per fox, including previously inhabited dens revisited by the same fox, between years and among the 3 seasons using 2-way ANOVA. Second, we examined the seasonal rate of new den use by comparing only the number of new dens occupied by each fox, also using 2-way ANOVA. If the season × year interaction was not statistically significant, data were combined and a 1-way ANOVA was used to compare den use among seasons. Analyses were considered statistically significant if $P \leq 0.05$

Habitat condition at each den site was assessed in a 5-m-radius circle (78.5 m^2), centered over the central den entrance, during June and July of each year. In a network of dens with many openings, the entrance that appeared to have most use was classified as the central entrance. Caved-in entrances were not tallied. A den was classified as a natal den based on presence of pup scat or observation of pups at the den site. Mean and standard error were determined for physical characteristics, including height and width of the central entrance and number of entrances at each den.

We categorized surrounding habitat as creosote, grass, mesquite, tarbush, saltbush, or a combination of these types, based on visual assessment of predominant vegetation. Identifying and counting each stem within the circle assessed density of surrounding vegetation. Relative percent cover was estimated at 4 points, randomly placed along a 5-m radius in each cardinal direction. At each point cover was estimated using a 0.8-m^2 circular sampling point frame. Vegetation was classified as shrub, grass, cactus, or yucca. Percent cover of litter, lichen, and bare sand was also estimated. The 4 cover measurements were averaged for analysis. Mean and standard error of stem counts within the sampling radius were determined to compare vegetation density surrounding dens. Mean percent of total vegetative cover was determined in addition to mean percent of cover for shrub, grass, yucca, cactus, sand, litter, and lichen. We compared all variables between natal and non-natal dens using t tests and considered analyses statistically significant if $P < 0.10$.

A global positioning system was used to determine Universal Transverse Mercator (UTM) coordinates at 94 den sites. UTM coordinates were input into a geographic information system (GIS; ArcInfo) and plotted on a soil survey map. Land slope and aspect at each den site were determined using digital topographic maps in GIS format. The proportion of dens present within each soil type, slope, and aspect class was analyzed relative to availability of those classes in the 53-km^2 study area using chi-square analysis. Den opening orientation was classified as north, northeast, east, southeast, south, southwest, west, or northwest and tested using a chi-square test. Dens with missing data were censored from analyses for that variable but remained in the analysis for remaining variables.

RESULTS

We captured 20 kit foxes (14 females, 6 males) during 1680 trap-nights in 1994 and 1995. During the study period we observed 7 different mated pairs. Based on 480 radiolocations, 116 non-natal and 16 natal dens were located. Mean number of den site changes did not differ within seasons between years ($P = 0.84$). When each year was combined, the rate of den site changes did not vary seasonally ($P = 0.28$; Fig. 1). The number of new dens used within each season did not differ between years ($P = 0.99$). Therefore, years were combined and we found that kit fox used more new dens during breeding and pup-rearing seasons ($P = 0.05$; Fig. 2).

Natal dens did not differ from non-natal dens with few exceptions (Table 1). Natal den entrances were taller than non-natal den entrances ($P = 0.01$). Overall, den entrance heights were significantly larger than widths ($P < 0.01$). Vegetative characteristics did not differ between natal and non-natal dens, although mean percent vegetative cover tended to be greater around natal dens ($P = 0.10$). Cactus species were more abundant around non-natal dens ($P = 0.02$).

Kit foxes on McGregor Range denned more frequently than expected in creosote habitat associations, relative to availability ($P < 0.01$; Fig. 3). Small sample sizes precluded statistical analysis of habitat differences between natal and non-natal dens. Kit foxes denned more frequently than expected within the Mimbres-Tome soil series association in relation to its availability ($P < 0.01$). Ninety-four percent ($N = 88$) of kit fox dens were located within this series, which is well drained and occurs throughout lowlands. Slope is less than 5% and flooding may occur periodically. Predominant vegetation associated within this series is creosote bush. Most soil within this association is

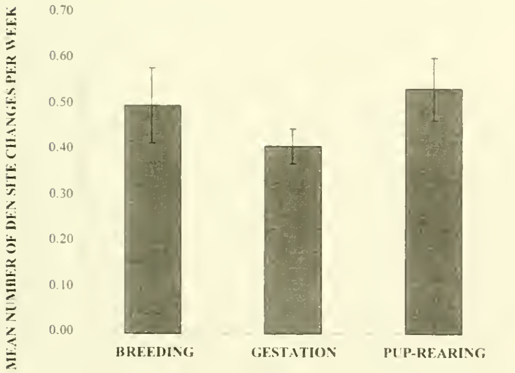

Fig. 1. Mean and standard error number of den site changes per week by kit foxes during breeding, gestation, and pup-rearing seasons in the northern Chihuahuan Desert, Fort Bliss Military Reservation, New Mexico, 1994 and 1995.

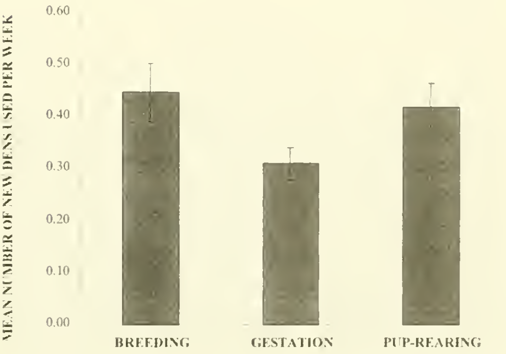

Fig. 2. Mean and standard error number of new dens used per week by kit foxes during breeding, gestation, and pup-rearing seasons in the northern Chihuahuan Desert, Fort Bliss Military Reservation, New Mexico, 1994 and 1995.

TABLE 1. Physical and vegetative characteristics of natal and non-natal kit fox dens on Fort Bliss, Otero County, New Mexico, 1994–1995.

Characteristic	Non-natal dens (mean ± $s_{\bar{x}}$)	N	Natal dens (mean ± $s_{\bar{x}}$)	N	P-values
Mean den entrance height (cm)	19.9 (0.4)	116	22.9 (1.5)	16	0.01
Mean den entrance width (cm)	18.7 (0.4)	116	19.6 (0.1)	16	0.18
Mean number of den entrances	1.9 (0.2)	116	2.0 (0.3)	16	0.39
Mean percent shrub cover	13.4 (1.5)	80	14.0 (0.3)	15	0.44
Mean percent yucca cover	0	80	1.3 (0.3)	15	0.17
Mean percent cactus cover	0.1 (0.1)	80	0	15	0.02
Mean percent grass cover	19.6 (1.7)	80	23.7 (4.0)	15	0.19
Mean percent sand cover	52.9 (1.8)	80	45.5 (4.0)	15	0.05
Mean percent litter cover	11.5 (1.3)	80	10.5 (2.1)	15	0.37
Mean percent lichen cover	5.0 (1.0)	80	6.1 (1.9)	15	0.34
Mean percent total vegetative cover	31.4 (1.4)	80	38.6 (5.1)	15	0.10
Shrub density (stems per 78.5m^2)	46.2 (4.7)	106	32.6 (6.8)	15	0.28
Grass density (stems per 78.5m^2)	49.9 (4.7)	106	32.9 (10.3)	15	0.20
Yucca density (stems per 78.5m^2)	0.3 (0.2)	106	0.3 (0.3)	15	0.85
Cactus density (stems per 78.5m^2)	1.7 (0.4)	106	0.9 (0.4)	15	0.42

silty loam or silty clay loam in higher elevations and sandy loam in lower elevations (Derr 1981). There were several soil associations within the study area in which no dens of radio-collared kit foxes were located. These associations have steeper slopes, ranging from 5% to 20%, are more rocky, and may have been unsuitable for den excavation.

Eighty-five percent of the study area had minimal slope (0 to 1 degree). Kit fox dens were located in expected proportions within these slope classes (P = 0.93). Kit fox dens occurred more frequently than expected (P = 0.03) on slopes oriented to the northwest. Both natal and non-natal dens opened more frequently to the southeast and northwest (P < 0.01).

DISCUSSION

We found no seasonal variation in average number of kit fox den site changes. These results are consistent with previous studies of seasonal kit fox den use on a military installation in California (Reese et al. 1992). However, kit foxes used more new dens during breeding and pup-rearing seasons. Egoscue (1956) suggested that during the breeding season kit foxes may visit many occupied and unoccupied dens sites, possibly surveying for potential dens or a prospective mate. Egoscue (1956) also noted that on several occasions natal dens have been abandoned suddenly and the pups moved to a new den. Movement between natal dens has been attributed to predator avoidance, local depletion of food, or intolerable flea levels (Egoscue 1956). Such behaviors may have contributed to the greater number of new dens used per fox during these seasons.

Kit foxes often den with a mate or in a social group; therefore, there may be a lack of independence in den use among individual foxes. Within this study no groups of 3 or more radio-collared foxes were located, and paired radio-collared kit foxes were found in the same den in only 20% of total locations. Although we did not account for autocorrelation in our analysis, we recognize that we may have underestimated the average number of new dens due to the presence of mated pairs in our sample.

Our results suggest that natal and non-natal dens are quite similar on McGregor Range. The only distinguishable feature is central den entrance height. Furthermore, a "keyhole" shape (e.g., greater height than width) characterized all den entrances. We believe this shape may allow quick entrance by kit foxes while impeding entrance of predators such as coyotes (*Canis latrans*) or badgers (*Taxidea taxus*; Egoscue 1962, Berry et al. 1987, Reese et al. 1992). Dens provide escape cover throughout the year but are especially important during the pup-rearing season when pups are most vulnerable.

Kit foxes selected sites most frequently in creosote habitat associations. Denning habitat in general was characterized by relatively short, patchy vegetation. These results concur with

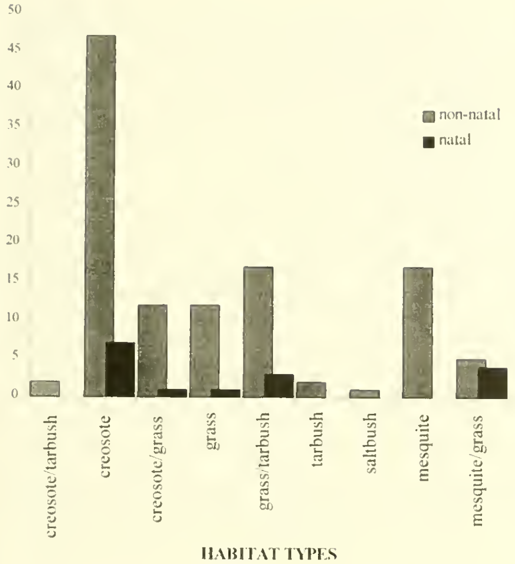

Fig. 3. Number of kit fox dens by habitat type in the northern Chihuahuan Desert, Fort Bliss Military Reservation, New Mexico, 1994 and 1995.

previous studies examining kit fox habitat utilization throughout their range (Egoscue 1956, 1962, O'Farrell 1987, Zoellick et al. 1989). Egoscue (1962) stressed the importance of creosote habitat for den sites in the Great Basin and suggested that kit foxes utilize adjacent sandy dune habitat in Utah for foraging. Both kit and swift foxes have demonstrated an ability to adapt to open habitats including creosote flats and grasslands with low and sparse vegetation. These adaptations may allow small foxes to more efficiently detect predators such as coyotes and bobcats (*Felis rufus*; Zoellick et al. 1989).

We found characteristics of soil and terrain used as denning habitat similar to those reported in previous studies. Kit and swift foxes typically den in loose, sandy, and well-drained soils (Hall 1946, Cutter 1958, Egoscue 1962, O'Neal et al. 1987, Zoellick et al. 1989, Reese et al. 1992). Past studies indicate dens are often located on gentle to moderate slopes (Egoscue 1956, Morrell 1972, Berry et al. 1987).

Kit fox dens were located on slopes with a northwest aspect more than expected, and den openings were more frequently oriented toward the northwest and southeast. Previous studies suggest that direction of den opening may reflect the prevailing orientation of slopes in the area (Berry et al. 1987). While aspect may confer special advantages for dens, direction of den opening may be related to site-specific conditions such as vegetation, drainage, or climate. Den orientation for red fox (*V. vulpes*) on Assateague Island, Maryland, is often associated with local prevailing wind directions (Krim et al. 1990). Cheesemore (1969) found that most arctic fox (*Alopex lagopus innuitus*) den entrances had a southerly, easterly, or westerly orientation, possibly indicating a preference for a warmer exposure. If orientation is related to wind and microclimate, it is possible that kit foxes orient their dens toward a cooler northern exposure. We did not, however, assess any microclimatic variables.

Recognition of kit fox dens and denning habitat may be useful to the military in making land-use decisions and assessing potential impacts of activities on the environment. Previous studies of the effects of military activities discovered that vehicles had damaged several dens, but kit foxes were not trapped inside the dens (Berry et al. 1992). On our study site we did not observe direct impacts resulting from military activity on any surveyed dens. Additionally, there was no evidence of damage to dens from live-fire exercises. However, we had limited access to designated impact zones to fully document effects of such use in this area.

Berry et al. (1992) suggest that numerous dens sites provide adequate shelter and protection for kit foxes while allowing for the destruction of several dens without adversely impacting fox populations. Because kit foxes change dens at a constant rate throughout most of the year, and we do not know why they change their den sites, we view dens as important to population survival. None should be considered surplus. Further, because few traits distinguish natal from non-natal dens, we recommend that all dens be considered potential natal dens. Although military activities do not adversely impact den sites on our study area, off-road activities hold the greatest potential for inadvertent impacts to dens or suitable denning habitat. Careful consideration should be given to intensity of off-road activities in potential kit or swift fox habitat.

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ECOLOGY OF FLANNELMOUTH SUCKER IN THE LEE'S FERRY TAILWATER, COLORADO RIVER, ARIZONA

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ABSTRACT.—We investigated ecology of flannelmouth sucker (*Catostomus latipinnis*) from 1992 to 1997 in the 26-km Lee's Ferry reach of the Colorado River immediately below Glen Canyon Dam, Arizona. We captured by electrofishing a total of 212 fish and recaptured 52 previously tagged by others. Flannelmouth sucker were captured throughout the tailwater but tended to aggregate within about 5 km of the dam, possibly reflecting blockage of historic migration routes. Catch per hour of electrofishing did not differ among years but was greater from November to February than other periods, suggesting seasonal movements of flannelmouth sucker into the tailwater. Mean lengths and weights of fish did not differ among years or seasons. Length frequency analyses also indicate there were no significant yearly trends in proportion of catch within size classes of fish. Mean condition differed only among seasons and was greatest in February, lowest in August, coinciding respectively with pre- and post-spawning periods of flannelmouth sucker in a tributary just downstream from Lee's Ferry. Recaptured fish migrated from initial tagging locations 1.4–231 km downstream from Lee's Ferry. Fifty-nine percent of recaptured fish with known initial tagging locations increased in length, and fish tagged initially as subadults or adults, respectively, grew an average of 45.9 mm and 5.5 mm per year.

Key words: flannelmouth sucker, movement, distribution, life history, native fish, regulated river, Colorado River.

Native fishes in the Colorado River below Glen Canyon Dam (GCD), Arizona, declined in abundance following emplacement of the hydroelectric facility in 1963 (Minckley 1991). Flannelmouth sucker (*Catostomus latipinnis*) is one of the long-lived native species (Scoppetone 1988) endemic to the Colorado River drainage and persists in Glen and Grand canyons and much of the upper Colorado River basin (Minckley 1991). Flannelmouth sucker aggregate in tributaries and associated inflow areas of Glen and Grand canyons (Robinson et al. 1996, Douglas and Marsh 1998, Weiss et al. 1998) and historically were abundant within the Glen Canyon tailwater and downstream (Holden and Stalnaker 1975). Weiss et al. (1998) suggested that an increase in mean lengths of flannelmouth sucker spawning in the Paria River between 1981 and 1993 indicated an aging population with relatively low recruitment to sexual maturity. Although categorized as a species of concern by the U.S. Fish and Wildlife Service (1994), little is known about ecology of flannelmouth sucker (McAda and Wydoski 1985, Douglas and Marsh 1998, Weiss et al. 1998). The species spawns in spring (Douglas and Marsh 1998, Weiss et al. 1998) and migrates long distances (Chart and Bergersen 1992), but temporal distribution and movements are poorly understood. In this study we examined distribution, movements, structural indices, and trends of flannelmouth sucker in the Glen Canyon tailwater (Lee's Ferry reach) during long-term monitoring.

STUDY SITE

Glen Canyon Dam impounds the Colorado River near the Arizona-Utah border and forms Lake Powell, a 653-km^2 meromictic reservoir. Lee's Ferry reach is confined within Glen Canyon between the dam (river kilometer [RK] –26) and Lee's Ferry (RK 0). Hypolimnetic releases from the reservoir are clear and cold (Stanford and Ward 1991, Shannon et al. 1996, Stevens et al. 1997). More stable operating regimes for GCD were initiated in 1991, following decades of widely variable releases from the dam (Marzolf 1991, Patten 1991). Releases from GCD during the present study generally ranged between about 142 m^{3}s^{-1} and 708 m^{3}s^{-1}, with daily variations not exceeding ca 227 m^{3}s^{-1}. Other fishes in the Lee's Ferry reach are nonnative rainbow trout (*Oncorhynchus mykiss*) and common carp (*Cyprinus carpio*).

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TABLE 1. Catch per hour (CPUE) of electrofishing (EF) and numbers of recaptures (*N*) for flannelmouth sucker in the 26-km Lee's Ferry reach, Colorado River, 1992–1997.

Year	No. trips	Total EF (hr)	Total catch	CPUE	Recapture (*N*)
1992	4	33.3	72	2.2	2
1993	2	16.7	11	0.7	0
1994	3	25.0	33	1.3	4
1995	2	16.7	53	3.2	9
1996	4	33.3	26	0.8	5
1997	3	15.0	17	1.1	5

Materials and Methods

We electrofished 9–15 fixed transects (ca 2000 sec/transect) randomly placed throughout Lee's Ferry reach between dusk and dawn during 19 trips between February 1992 and December 1997. We electrofished 2–4 times per year (Table 1) and collected samples in all months except January, June, and October (Table 2). We captured flannelmouth sucker using single-pass electrofishing (EF) from an aluminum boat equipped with a Coffelt CPS Mark XX electrofishing unit (Coffelt Manufacturing, Flagstaff, AZ). We employed a complex pulsed system of direct current, applying 215 volts and maintaining a 15-ampere output to a 30-cm-diameter stainless steel anode system (Sharber et al. 1994). We examined fish for previous marks, measured to the nearest millimeter (total body length [TL]), weighed to the nearest gram, injected with a passive integrated transponder (PIT) tag (if none present), and released all fish near capture points. Catch-per-unit-effort (CPUE), computed as the number of fish caught per hour of EF with electrical current in the water, was considered an index of population abundance.

We compared log-transformed weight/length relationships between sexes using a 2-sided *t* test. Mean condition factor ($K = W^5/L^3$), TL and weight among months and years, and seasonal groupings of catch/transect/trip were compared using the Kruskal-Wallis test. Spearman's Rank Order correlation coefficients were calculated to quantify relationships between recapture among months and years and CPUE and size structure among years. Statistical significance was determined at $\alpha = 0.05$ for all tests. We estimated growth rates of fish by subtracting lengths at initial capture from those at recapture and dividing by elapsed time (yr) between capture and recapture. We defined distance moved as displacement of recaptured fish from locations where they were marked initially to last point of recapture. We assumed that adult and subadult flannelmouth sucker, respectively, were ≥390 mm and <390 mm in length (McAda and Wydoski 1985).

Results

We captured a total of 212 flannelmouth sucker (range 404–646 mm TL) during 19 trips between 1992 and 1997. No fish were captured in September 1993. The highest percentage of fish were 451–500 mm TL (Fig. 1). Most fish (54%; 114/212) also were captured within 4.8 km of Glen Canyon Dam, and 12% (25/212) were captured near a gravel bar at RK –6.6, most (11%; 24/212) during April or May. Mean lengths and weights did not differ significantly among years or months (Table 2). Catch-per-unit-effort ($N = 6$; mean $= 0.9 \pm 0.2\ s_{\bar{x}}$) varied widely among years (Table 1), and no significant year-to-year trend was evident (Spearman Rank Order correlation, $R = -0.14$). However, catch-per-unit-effort differed significantly ($P = 0.011$) among seasons and was greater from November to February ($N = 6$; mean $= 1.4 \pm 0.2\ s_{\bar{x}}$) than March to May ($N = 8$; mean $= 0.6 \pm 0.2\ s_{\bar{x}}$) or July to September ($N = 4$; mean $= 0.6 \pm 0.3\ s_{\bar{x}}$). Proportion of catch for individual length classes also did not differ among years (Spearman Rank Order correlations for fish 400–450 mm, 451–500 mm, 501–550 mm, 551–600 mm, and >600 mm TL, respectively, were $R = -0.12$, $R = -0.09$, $R = 0.60$, $R = -0.66$, and $R = -0.07$).

Sex ratio (male:female) was 3.3, based on 52 fish for which gender was determined (manual expression of gametes). Range in length for reproductively mature males and females, respectively, was 421–518 mm and 464–646 mm. Both length and weight data were collected for 30 of these fish, and we found no difference ($P = 0.4412$) in log-transformed

TABLE 2. Mean (± $s_{\bar{x}}$) monthly total lengths (mm), weights (g), and condition factors (K) for flannelmouth sucker captured by electrofishing in the 26-km Lee's Ferry reach, Colorado River, 1992–1997. N = number of observations.

	Length			Weight			K		
Month	N	Mean	$s_{\bar{x}}$	N	Mean	$s_{\bar{x}}$	N	Mean	$s_{\bar{x}}$
Feb	19	495	7	19	1345	66	19	1.10	0.03
Mar	19	494	13	19	1253	83	19	1.03	0.04
Apr	11	508	10	11	1371	77	11	1.04	0.03
May	37	496	8	15	1512	140	15	1.08	0.02
Jul	4	496	11	4	1274	102	1	1.04	0.05
Aug	26	518	22	26	1227	58	25	0.97	0.02
Sept	2	468	4	2	1114	146	2	1.12	0.12
Nov	30	501	7	31	1363	54	30	1.09	0.02
Dec	61	503	5	61	1389	45	61	1.07	0.01
All years	209	502	4	188	1348	25	186	1.06	0.01

weight-length relationships between sexes. Weight-length relationships indicated that growth was approximately isometric (logW = –4.350 + 2.7665logTL). Mean K, which also did not differ significantly among years, differed ($P < 0.05$) among months and was greatest in February (except for September, when only 2 fish were caught) and lowest in August (Table 2).

There were no multiple recaptures, and cumulative recapture of fish previously tagged was 12% (25/212). Proportion of recaptured fish did not vary significantly among years (Table 1; Spearman Rank Order correlation, R = 0.60) or months (Spearman Rank Order correlation, R = 0.36). Total length of recaptured fish was 420–582 mm. Seventeen fish were recaptured for which original tagging information is known (Table 3). Thirty-five percent (6/17) were tagged initially in or near the Little Colorado River (RK 98), and 53% (9/17) were tagged in the Paria River or its confluence with the mainstem Colorado River (RK 1.4). One recaptured fish was tagged initially near Kanab Creek (RK 231) and another in the Lee's Ferry reach at RK –22.9 in 1992; the latter was recaptured at the same location in 1995 (Table 3). Mean distance of capture from initial marking location for the 17 fish was 52 ± 17 $s_{\bar{x}}$ km (range 1.4–231 km). All fish tagged as subadults (N = 3) moved 98 km from tagging location to recapture site, and those tagged as adults moved between 1.4 km and 231 km (N = 14; mean 49 ± 20 $s_{\bar{x}}$; Table 3). Nearly 2/3 (64.7%; N = 11) of recaptured fish were caught in November–December (Table 3).

Fifty-nine percent (10/17) of recaptured fish for which location of initial tagging was known grew in length, and 81% (13/16) increased in weight after initial tagging (Table 3). Thirty-five percent (6/17) of recaptured fish reflected negative growth, and 6% (1/17) showed no growth. Mean growth rate of fish that grew and were marked initially as adults was 5.5 ± 1.9 $s_{\bar{x}}$ mm/yr (N = 14; range 1.9–12.8 mm/yr), and mean growth rate for fish marked as subadults (189–365 mm TL) was 45.9 ± 16.8 $s_{\bar{x}}$ mm/yr (N = 3; range 25.7–79.3 mm/yr).

DISCUSSION

Our results support the conclusion (Chart and Bergersen 1992) that adult flannelmouth sucker are tolerant of cold tailrace habitats. We suggest that flannelmouth sucker in the Lee's Ferry reach comprised a mobile aggregation of fish of presumed sexual maturity (McAda and Wydoski 1985, Weiss et al. 1998). In our study CPUE differed among seasons and locations but not among years, suggesting generally stable densities of flannelmouth sucker in Lee's Ferry reach between 1992 and 1997. Douglas and Marsh (1998) also concluded that the flannelmouth sucker population in the Little Colorado River and its confluence with the Colorado River was stable during 1991–1995.

Our results agree with previous observations of long-distance movements by flannelmouth sucker (Chart and Bergersen 1992). Forty-one percent of our recaptures for which original tagging information was known were originally marked between 98 km and 231 km downriver from Lee's Ferry. Long-distance seasonal migrations may be integral to life history of flannelmouth sucker (Chart and Bergersen 1992) and

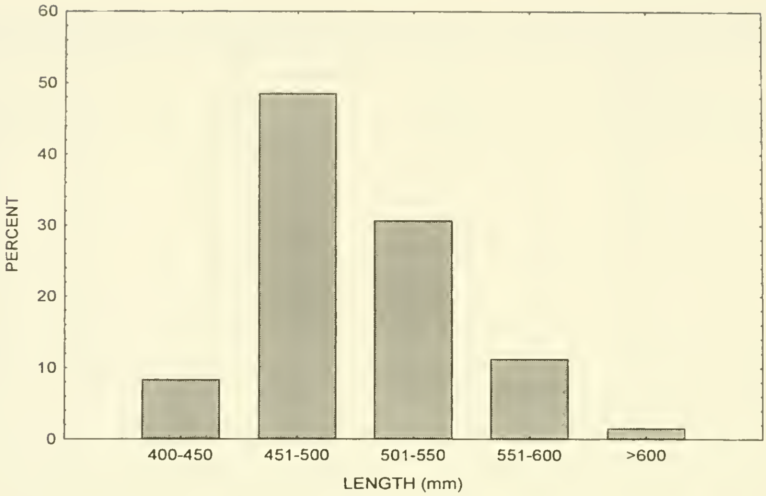

Fig. 1. Length-frequency distribution (percent of total catch by length classes; $N = 212$) of flannelmouth sucker captured by electrofishing in the 26-km Lee's Ferry reach, Colorado River, 1992–1997.

other large-bodied native fishes (Tyus and Karp 1990, Minckley 1991, Modde and Irving 1998). However, a portion of the population likely is sedentary, since 53% of recaptured fish for which original tagging information was known were marked initially in the Paria River or its confluence with the Colorado River (RK 1.4). The flannelmouth sucker population in the White River also was generally mobile, but some fish were sedentary (Chart and Bergersen 1992).

Flannelmouth sucker in our study were captured throughout Lee's Ferry reach from 1992 to 1997, but CPUE indicates they tended to aggregate near the dam and, prior to or during the spring spawning season (Weiss et al. 1998), near a mid-channel gravel bar in Lee's Ferry reach (RK –7). Flannelmouth sucker also aggregate just below Taylor Draw Dam on the White River (Chart and Bergersen 1992), and aggregation below dams may reflect blockage of historic migration routes used by native fishes (Holden 1991, Minckley 1991, Chart and Bergersen 1992). Movements (based on CPUE) of flannelmouth sucker into the Glen Canyon tailwater increased during late fall and winter and declined in spring and summer. Timing of seasonal increase in CPUE in Lee's Ferry reach corresponds with pre-spawning migration to the Paria River and its confluence with the Colorado River (Weiss et al. 1998) and is coincident with a seasonal decline in numbers in the Little Colorado River and its confluence area (Douglas and Marsh 1998).

We captured 83% of ripe females and 93% of ripe males during February–May, prior to or during Paria River spawning (Weiss et al. 1998). We found a sex ratio (male:female) of 3:1 in Lee's Ferry reach, while Weiss et al. (1998) reported sex ratios of about 2:1 for spawning flannelmouth sucker in the Paria River and Bright Angel Creek and about 1:1 at Paria River confluence with the Colorado River. Forty-two percent of fish we captured were <490 mm, at which length McAda and Wydoski (1985) reported all flannelmouth sucker were reproductively mature. Flannelmouth sucker caught in Paria River spawning areas ranged from 385 mm to 580 mm (Weiss et al. 1998), and we found that reproductively mature fish ranged from 421 mm to 646 mm. Mean length of fish we captured equaled that of flannelmouth sucker caught in the mouth of the Paria River and was greater than mean length of fish captured on upstream spawning areas in the tributary (Weiss et al. 1998).

Average length of spawning flannelmouth sucker in the Paria River increased between 1981 and 1983, possibly indicating low recruitment to reproductive maturity and an aging population (Weiss et al. 1998). However, we found no evidence supporting the hypothesis of an aging population; mean lengths and weights and size structure of fish did not differ

TABLE 3. Date, location of initial tagging (RK = river km), total length (TL = mm), weight (W = g), and computed growth rates (CG = mm/yr) for flannelmouth sucker recaptured by electrofishing in the Lee's Ferry reach, Colorado River, 1992–1997. YAL = years between initial tagging and recapture.

	Initial Tagging			Recapture					
Date	TL	W	RK	Date	TL	W	RK	YAL	CG
2-12-86[a]	516	1349	1.4	8-26-92	532	1263	–8.6	6.5	2.5
10-14-92[c]	443	888	98	3-25-96	455	960	–3.0	3.4	3.5
10-16-92[c]	365	462	98	12-7-94	420	856	–6.5	2.1	25.7
11-11-92[a]	461	1093	–22.9	12-4-95	468	1136	–23.7	3.1	2.3
3-6-93[c]	189	54	98	8-27-96	464	1024	–20.8	3.5	79.3
3-29-93[b]	558	2000	1.4	12-6-95	565	2062	0	3.7	1.9
4-8-93[b]	527	1400	1.4	5-14-95	524	—	–6.5	1.1	–2.7
4-22-93[a]	404	677	231	12-6-97	499	1325	–17.5	7.4	12.8
4-8-93[b]	543	870	1.4	12-7-94	525	1579	–8.6	1.7	–10.5
5-10-93[b]	4854	1170	1.4	12-6-94	480	1145	–20.8	1.6	–3.1
5-10-93[b]	508	1120	1.4	12-6-95	500	1236	0	1.6	–5.0
5-16-93[a]	464	976	98	12-6-97	499	1686	–17.5	2.7	12.8
7-8-93[b]	467	1150	1.4	12-4-95	467	1232	–23.7	1.4	0
8-18-93[b]	588	2000	1.4	12-4-95	582	2077	–23.7	2.3	–2.6
3-18-94[c]	422	700	98	5-13-95	425	761	–20.8	1.2	2.6
7-7-94[c]	361	376	98	9-1-97	464	998	–5.0	3.2	32.7
3-20-96[b]	529	1803	1.4	11-19-96	525	1850	–20.8	1.7	–2.4

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[b] University of Arizona
[c] Arizona State University

among years. Electrofishing may overestimate abundance of larger fish and not accurately represent the size distribution of a population (Reynolds 1996), but the high proportion of small adults (≤500 mm) in our study and recapture of fish marked initially as subadults in Grand Canyon suggest that recruitment to sexual maturity is occurring. We captured no subadults, based on a minimum length at maturity of about 390 mm (McAda and Wydoski 1985, Weiss et al. 1998). Movement of flannelmouth sucker into the cold, clear-water Lee's Ferry reach may not occur until about reproductive maturity (Weiss et al. 1998).

Our growth data are questionable due to small samples size and inaccurate measurements. However, patterns of growth for fish tagged originally as adults and subadults were comparable to those reported by McAda and Wydoski (1985). Slow growth rates of adults in Lee's Ferry reach might be explained by senescence or influences of cold water temperatures and inadequate food resources, as suggested for other species (Vanicek and Kramer 1969, Weatherly 1972, Kaeding and Osmundson 1988). However, size structure of fish we recaptured does not indicate senescence, since it remained comparable over time and indicated a high proportion of small adults. Inadequate food resources also seem unlikely. Flannelmouth sucker feed on benthic macroinvertebrates (Minckley 1991), and secondary producers are abundant in Lee's Ferry reach (Blinn et al. 1995, Shannon et al. 1996, Stevens et al. 1997). Moreover, condition of fish was comparable among years. The 1992–1997 period was characterized by higher minimum and more stable releases than previously from GCD (Marzolf 1991, United States Department of Interior 1995), possibly benefiting flannelmouth sucker (Blinn et al. 1995, Stevens et al. 1997). However, our results fail to support this hypothesis, since mean densities, lengths, weights, and condition of flannelmouth sucker did not differ over the 6-yr study. Electrofishing also might contribute to slower growth of shocked individuals (Dalbey et al. 1996, Thompson et al. 1997), but only 1 fish we recaptured likely was captured initially by electrofishing, and its computed growth rate was near the adult mean.

Between 1984 and 1997 nearly 1000 flannelmouth sucker were marked and released in Lee's Ferry reach, and 9000 or more likely were marked and released at downriver locations. During 6 yr of electrofishing, we recaptured 25 fish, none of which was a multiple recapture, and only 1 was tagged originally in the Lee's Ferry tailwater. Our cumulative recapture of 12% was comparable to that reported by Chart and Bergersen (1992) for the White River. Douglas and Marsh (1998), using seines and hoop-and-trammel nets in or near spawning areas in Little Colorado River, reported higher recapture rates. Catch rates and size structure of the mobile flannelmouth sucker aggregation in Lee's Ferry reach showed no differences annually between 1992 and 1997, and capture of fish tagged initially as subadults suggests that recruitment to reproductive maturity occurred. We hypothesize that population trend was stable between 1992 and 1997 and that more stable flow regimes during this period had no influences on densities or size structure of the aggregation. Further studies of flannelmouth sucker in Lee's Ferry reach, as well as tributaries (Weiss et al. 1998), will enhance assessment of population trends and allow resource managers to evaluate long-term influences of dam operations on this native species.

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HABITAT USE AND SUBSPECIFIC STATUS OF MERLINS, *FALCO COLUMBARIUS*, WINTERING IN CENTRAL UTAH

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ABSTRACT.—Most ornithological literature for Utah reports the status of the Merlin (*Falco columbarius*) as rare or scarce. Only the most recently published checklists (Behle and Perry 1975, Behle et al.1985) record it as uncommon. Likewise, a 1998 printed checklist (Utah Ornithological Society 1998) lists it as uncommon. Also misrepresented in the literature are the status and distribution of the 3 rather distinct subspecies, each of which occupies dissimilar habitats during the breeding season. We made random observations of Merlins in northern Utah beginning in the 1950s and then studied them continuously between 1992 and 1997 in Utah County, Utah. During the 1992–1997 period, we were able to clearly allocate 95 males and 76 females to subspecies, including within our count 58 falcons trapped (some fitted with radio telemetry). The winter habitat in which they occurred was categorized as either *urban* (mainly dense residential area) or *rural* (agricultural lands, dairy farms, or scattered homes). There was a statistically significant ($\chi^2 < 0.001$) difference in habitat use, with the boreal forest–breeding *F. c. columbarius* frequenting urban areas 68% of the time, and prairie parkland–breeding *F. c. richardsonii* frequenting rural habitats 78% of the time.

Key words: Merlin subspecies, winter habitat use, Falco columbarius richardsonii, Falco columbarius columbarius, Falco columbarius suckleyi.

Checklists of the birds of Utah from half a century ago (Behle 1944, Woodbury et al. 1949) indicated that the Merlin (*Falco columbarius*) was a rare to sparse migrant and winter visitant in Utah. There was also some uncertainty as to the frequency of each subspecies occurring in Utah. The Behle (op. cit.) and Woodbury et al. (op. cit.) checklists summarized records from numerous government expeditions to Utah in the mid- to late 1800s, indicating that those early expeditions likewise did not report many Merlins. However, one would not necessarily expect the early expeditions to encounter Merlins because much of their time in Utah was during the summer months (see Behle 1990). Twomey (1942), who worked in the Uinta Basin of eastern Utah, indicated that he saw Merlins only as migrants in May and September; he allocated them to *richardsonii* but had no specimens to verify his determination. Our guess is that Twomey did so based on the proximity of the Uinta Basin to Colorado where *richardsonii* was conventionally thought to be the most frequently recorded subspecies (e.g., of 30 specimens in the Denver Museum of Natural History in 1965, 21 were *richardsonii;* Bailey and Niedrach 1965). Nonetheless, Merlins in fact were not often seen by ornithologists or bird watchers in the 1st half of this century even though an active Audubon Society was established in Utah and several graduate students in ornithology were pursuing degrees at Utah State University, University of Utah, and Brigham Young University; the former 2 especially had active programs in the 1940s–1960s. One of us (CMW) looked diligently for Merlins in the late 1940s and 1950s but saw few other than some shot in Tracy Aviary in Salt Lake City.

Three or 4 of the several falconers in Utah in the 1940s–1960s caught a few Merlins for their sport, but they spent considerable time looking for the ones they captured. One excellent ornithologist, bird observer, and falconer, Boyde Shaffer, worked at Tracy Aviary in Salt Lake City. During approximately 15 yr (late 1940s–1950s) he saw perhaps 8–10 Merlins and had 3 in the hand (all of the birds he called *F. c. columbarius*) in the aviary (where Merlins were attracted because of abundant House Sparrow [*Passer domesticus*] and other small bird populations and perhaps because public aviaries are "raptor sinks"; B. Schaffer personal communications). It was not until Behle and Perry (1975) and Behle et al. (1985) published their most recent checklists that the

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species was recognized to be uncommon, but widespread and regular in occurrence rather than scarce, in part because of work by many falconers and graduate students (see comments in White 1994). Likewise, the 1998 printing of the checklist (Utah Ornithological Society 1998) lists it as uncommon. Further, following the mid-1960s, although lacking good empirical data, it seemed to CMW that there was some habitat partitioning by subspecies; it is this aspect of habitat use and subspecies frequency that we studied and discuss below.

METHODS

Between 1992 and 1997 we noted habitat use in north central Utah for all individuals ($n = 171$) seen whose wintering home range habitats were identified by telemetry, repeated sightings of banded birds, or other distinct individuals occupying given locations over some period. These individuals were subjectively assigned to *urban* or *rural* categories based on the areas most frequented. Urban was defined as densely populated residential areas with some distinct business district. These areas usually contain many large trees, both deciduous and coniferous. Rural was defined as primarily agricultural areas with small townships, dairy farms, and occasional scattered residences. Frequently rural areas have considerable open landscapes, but they also may contain scattered large cottonwood trees.

Fifty-eight individuals were trapped and examined in the hand. Those not examined in the hand were, for the most part, able to be allocated to *richardsonii* (pale) or *columbarius* (dark), although there were some intermediates. *F. c. suckleyi* was generally most difficult to allocate confidently to subspecies unless in the hand. To allocate birds to subspecies, both in the hand and the museum, we used criteria set forth by Temple (1972a, 1972b). We surveyed an area of 910 km^2 on a weekly to biweekly basis (1992–1997), starting in late September and ending in early April of each year (see Haney 1997).

RESULTS

Merlins occupied all habitats (e.g., conifer forest, oak hillsides, riparian, etc., for night roosting in addition to those examined during daylight) within the area in 1992–1997, with nearly equal numbers encountered in both urban ($n = 78$) and rural ($n = 93$) areas (Table 1), although rural locations covered more area. All individuals identifiable with radio transmitters or by distinctive physical features predominantly used one habitat or the other with little overlap into the other category. All subspecies and sexes trapped or identified (some with bands) occurred in urban and rural areas except *richardsonii* females, which were found only in rural areas (Table 1). *F. c. columbarius* mostly used urban areas, and *richardsonii* rural areas (χ^2, $P < 0.001$), while *suckleyi* (perhaps in part because the sample size was so small) showed no specific area use. Male *F. c. columbarius* was found mostly in urban areas ($\chi^2 = 8.8$, $P < 0.01$), while male *richardsonii* showed a tendency to use rural areas ($\chi^2 = 3.6$, $P \approx 0.6$). Specific areas within cities and certain cattle feedlots in rural areas were occupied by Merlins every season. Overall, males occurred slightly more often in urban than rural areas, and females twice as often in rural as in urban areas. Of particular note were *richardsonii* females, 100% of which were located in rural areas (Table 1).

TABLE 1. Winter habitat utilization indicating numbers of identified Merlins by subspecies and sexes in that habitat, winters 1992–1997.

Subspecies	Location	
Sex	Urban[a]	Rural[b]
F. c. columbarius		
Males	30	11
Females	21	13
TOTALS	51	24
F. c. richardsonii		
Males	17	30
Females	0	32
TOTALS	17	62
F. c. suckleyi		
Males	5	2
Females	5	5
TOTALS	10	7
TOTALS	78	93

[a] Treed neighborhoods with densely populated residential areas and small business districts

[b] Primarily agricultural areas with small townships, dairy farms, and occasional scattered residences and with considerable open landscapes

Of 218 individuals (including those identified in the field and museum specimens), 128 (59%) were males and 90 females (41%). There was a statistically significant difference between the numbers of each sex ($\chi^2 = 6.31$, $P < 0.025$), suggesting a slight male bias. DLH found that

Merlins wintering in northern California near Eureka (1984–1987) were nearly all females; males were seen only during autumn and spring migrations. In the greater Los Angeles area, however, DLH found that about 75% of Merlins were females, while inland in desert regions the ratios were reversed ($n \approx$ ca 100). These data taken together suggest some geographic habitat partitioning by sex (perhaps habitat partitioning within a given area?).

DISCUSSION

During the breeding season (roughly April to early September), *F. c. suckleyi* mainly occupies the cool, moist, conifer-forested coastal parts of the Pacific Northwest north of Vancouver Island to perhaps Prince William Sound, Alaska, and a short distance inland in British Columbia (perhaps 250 km, but range poorly defined in interior British Columbia; Campbell et al. 1990). The prairie-parkland *F. c. richardsonii* occurs in south central Canada and northern prairie states (formerly south to at least southwestern Wyoming) and occasionally in northern Colorado in juniper/ponderosa habitat (T. Ray, J.H. Enderson personal communications). (There is a summer record of an adult pair [breeding?] thought to be *richardsonii*, because of the pale dorsum, as far south as southern Utah in predominantly ponderosa pine habitat [Sailer 1987].) Much of the breeding habitat of *richardsonii* is aspen parkland, riparian, or open juniper/pine stands. Lastly, the largest geographical range is occupied by *F. c. columbarius*, and it occurs over the remainder of the boreal (taiga) and wooded portions (deciduous and coniferous) of North America from Newfoundland to Alaska north from the northern tier of the United States. Just where the southern edge of the Merlin's presumed breeding range occurs is poorly defined, and at least 1 set of purported Merlin eggs from the southern part of the range in the collection at the Western Foundation of Vertebrate Zoology was Sharp-shinned Hawks (*Accipiter striatus*; L. Kiff personal communication). Merlins in interior Alaska are of interest in that they appear more or less intermediate between *richardsonii* and *columbarius*, especially noticeable in the dorsal color of adult males (specimens, photographs, and personal observations).

Ornithological literature for most of the 20th century has recorded the presence or absence of species, frequently at the subspecies level, by the prolific publishing of records and checklists. That literature has been particularly faithful in recording 1st occurrences of species or subspecies in new geographical areas. There has been some virtue in doing this because it has helped in understanding distributional changes of the species at smaller population or geographic levels. Being able to discern geographic populations, regardless of one's view of the utility or reality of subspecies, has helped clarify the ebb and flow of species that in the end could be of conservation value. There are inherent flaws in that system, however. For such precision to function accurately, we must make several assumptions: (1) the intensity of observations has been constant through time, (2) the interest or number of observers has been constant, and (3) one can assign a subspecies category to specific individual birds.

Two examples will illustrate the utility of looking at the dynamics of distributional changes in populations by examining subspecies. California has a much longer and more intense history of ornithological observations than Utah, with an active specimen-collecting tradition. For California *F. c. richardsonii* was considered to be rare (Friedmann 1950), perhaps because there were only 9 specimen records from 1875 to 1944 (Grinnell and Miller 1944). However, DLH found *richardsonii* constituting about 5% of Merlins he has seen within the greater Los Angeles basin and about 45% in nearby high desert regions (combined $n \approx 100$), where Merlins are not uncommon during winter (M. Orr, J. LaGrone, S. Tucker, D. Cherry personal communications). In support of the findings of DLH, Grinnell and Miller (1944) suggested (in what seems to be an intuitive guess) that *richardsonii* may in fact be more common than the records indicate. Northward at Eureka, California, DLH counted only 5 *richardsonii* of 77 Merlins recorded. Unexpectedly, although only few Merlins are seen each year, nearly all in the low desert areas around Palm Springs and Palm Desert are female *suckleyi* (S. Tucker personal communications). For Utah, until about 1945, there were only 2–3 specimens classified as *richardsonii*. Today some 40–50% of all wintering Merlins trapped by falconers in Utah

(10–15 per yr) are *richardsonii* (K. Tuttle, A. Ross, P. Shane, R. Claude, D. Kessimakis, C. Monson, T. Roundy personal communications; personal observations). The 1st records of *suckleyi* (2 specimens) were from the early 1950s (Porter and Knight 1952) when those and a 3rd individual were obtained within a decade. Over the years no one has kept records on the possible percentage of *suckleyi* in the Utah population, but 4–5 individuals were identified each winter in Utah County alone between 1992 and 1997 (Haney 1997). These 2 examples from Utah and California, where a fair number of qualified people have been looking for Merlins in both states, suggest (1) that geographically different breeding populations have variably changing winter ranges, (2) that few Merlins were thoroughly examined earlier, or (3) that, in the case of Utah, both *richardsonii* and *suckleyi* were simply overlooked during all the work done from the mid-1800s to the 1960s. We suggest the former is the more accurate explanation for our results. Johnson (1994) provided many examples of western birds that have expanded their ranges over the latter half of this century, usually at the species level, concluding that changes occur from many causes. These 2 subspecies of Merlins may be other examples of that process.

Some of the earlier literature should be viewed with cautionary caveats, however. Knight's (1902) account of birds of Wyoming indicated that *richardsonii* was "locally . . . quite abundant" and that "during mild winters [it] probably remains." He suggested that the other type of Merlin (e.g., *F. c. columbarius*) was rare although it occurred on the Green River where specimens were taken (where *richardsonii* breeds). Later, McCreary's (1939) account of birds in Wyoming indicated that *F. c. columbarius* bred at Fort Bridger (although *richardsonii* actually breeds along the Green River only 70–80 km to the east). McCreary then compared *richardsonii*, which he indicated is the common form of Merlin in eastern Wyoming, with the Sharp-shinned Hawk, because of its superficial similarity with the sharp-shin. He then discussed Merlin specimens in the University of Wyoming collection. J.H. Enderson and CMW examined the specimens in that collection in 1962. Two of the specimens allocated to *richardsonii*, presumably by McCreary because his name was written on the museum label, were actually Sharp-shinned Hawks. It is not clear what happened in this case, but it simply might have been a lapse in writing tags or it may also suggest some confusion about statements on the status of *richardsonii* in Wyoming.

The University of Utah Museum of Natural History until 1985 contained about 10 specimens of Merlins, and other than the 3 *suckleyi* mentioned above, all were *F. c. columbarius* until CMW donated a *richardsonii* to that museum in the mid-1980s. The 1st recent record of a topotypical *richardsonii* was of an adult female (seen by CMW) captured on about 15 November 1968 by Dale Kessimakis and Marvin Meyer of Salt Lake City. Of the 57 Utah specimens of Merlins that have come into the M.L. Bean Life Science Museum at Brigham Young University (or that are elsewhere in the BYU Zoology Department), 27 (47%) are *columbarius*, 21 (37%) *richardsonii*, and 9 (16%) *suckleyi*. Most were acquired randomly after 1970; i.e., there was no selection for specific subspecies, with some donated by falconers and perhaps half of them coming from local rehabilitators after the birds died. Of the 8 specimens listed by Woodbury et al. (unpublished manuscript, of which Hayward et al. 1976 is a modified and shortened version) through 1945 for Utah, all except the reported *richardsonii* taken in the late 1800s (deposited in the Smithsonian Institution but unable to be located there now) were *F. c. columbarius*. Thus, the combined Utah data suggest to us that there has been a major shift eastward in wintering *suckleyi* and a similar westward shift in the wintering range of *richardsonii* (see American Ornithologists' Union [1957] that outlines subspecific ranges) and that in Utah the apparent increase in *richardsonii* may be related in some manner to its overall increase and expansion of range (Sodhi et al. 1993), especially in Canada (L. Oliphant personal communication).

Two hypotheses might explain subspecific habitat use on the nonbreeding ground in Utah (Table 1). Habitat preferences may be linked somewhat to structural habitat similarities with the breeding grounds. This may provide a familiar prey search image and hunting strategy. *F. c. columbarius* breeds in boreal forest regions, which have a high vertical structural component more similar to tree-covered urban areas in Utah County. *F. c. richardsonii* breeds in prairie regions of central North America that are dominated by vast open areas and are more similar to rural areas in Utah County. Also, such a notion is suggested by the findings of DLH in California. This concept of habitat similarity preference was derived independently by Sodhi and Oliphant (1992) during their studies of urban-nesting Merlins. They found that individuals of urban natal origins tended to hunt more in urban areas than did immigrants from other habitats.

Another hypothesis is that individuals are keying on preferred prey species that are similar to those on breeding grounds. Most prey studies have been done on breeding grounds, and they indicate specialization on 1 or 2 species of small birds (Sodhi et al. 1993). Horned Larks (*Eremophila alpestris*), the predominant prey of prairie populations of *richardsonii* (Fox 1964, Hodson 1978, Becker 1985), are numerous during winter in rural areas of central Utah. House Sparrows (*Passer domesticus*) are the predominant prey of urban breeders (Oliphant and McTaggert 1977, James and Smith 1987, Sodhi and Oliphant 1992) and are abundant in Utah urban areas.

There was no significant year-to-year difference in the ratio of males to females, which indicated a consistent male bias. But, based on the experience of DLH in California, there seemed to be regional habitat segregation perhaps related to prey-base differences. Another small falcon, the American Kestrel (*Falco sparverius*), shows sexual habitat segregation that has been attributed to the larger female forcing the smaller male into less suitable habitat that ultimately results in reducing winter competition (Koplin 1973, Mills 1976). There was no habitat component between sexes of Merlins. We were unable to determine sex ratios of the most migratory individuals going south to Central and South America, which would be instructive in helping to answer the question of whether there is consistent deferential sex movement. The only data we found indicating sex ratios in the Neotropics were in Blake (1977); he gives data on specimens he measured from the Neotropics as 53 males and 48 females (not significant, $\chi^2 = 0.25$). Based on sample sizes in his other species accounts, it appears that Blake did not simply try to use equal sample sizes for his measurements; thus, we assume Merlin numbers represent actual numbers collected. Of birds trapped in winter (and this may simply reflect trappability rather than different sex ratios) in Saskatoon, Saskatchewan, 32 (58%) of 55 were males, nearly the same as our percent difference although not significantly different (Warkentin et al. 1990). In the Netherlands, however, there were 70% more migrant females (from more northern origins) at winter communal roosts than males (Van Duin et al. 1984), again suggesting regional habitat segregation or further southward movement by males in that geographic location.

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HABITAT USE OF LEATHERSIDE CHUB (*GILA COPEI*) IN THE PRESENCE OF PREDATORY BROWN TROUT (*SALMO TRUTTA*)

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ABSTRACT.—The objectives of this study were to (1) examine distribution and habitat use of leatherside chub (*Gila copei*) in a creek with high densities of predatory brown trout (*Salmo trutta*), and (2) compare study results with published accounts of leatherside chub habitat use in streams with few or no brown trout. A 14-km section of Diamond Fork Creek, Utah, was point-shocked to determine macrohabitat (main channel and lateral habitat) and microhabitat (current, depth, substrate, and cover) use of leatherside chub. At the macrohabitat level, leatherside chub were most common in lower reaches of Diamond Fork Creek where the channel was braided and lateral habitats (cutoff pools and backwaters) were abundant. Only a single leatherside chub was found in the main channel of Diamond Fork. Investigations in other systems lacking brown trout indicated that leatherside chub occupy main channel habitats. At the microhabitat level, we found significant positive associations between presence of leatherside chub and both habitat depth and silt. In addition, we found a significant negative association between presence of leatherside chub and number of brown trout. Our results suggest predation by brown trout may limit leatherside chub to lateral habitats that could provide refugia against predation. The introduction of brown trout to systems with little lateral habitat could have serious effects on persistence of resident leatherside chub populations.

Key words: Gila copei, *leatherside chub, habitat use, predation,* Salmo trutta, *brown trout, Utah.*

The leatherside chub (*Gila copei*) is a small cyprinid native to eastern and southern parts of the Bonneville Basin of Utah, Wyoming, and Idaho (Sigler and Sigler 1987). As with other native fishes of the arid western United States (Deacon 1979), populations of leatherside chub have been severely impacted by man (e.g., impoundments, dewatering, siltation). In the Sevier River system of south central Utah, leatherside chub now occupy only 58% of their original range and have been extirpated from the Beaver River system (Wilson and Belk 1996).

Leatherside chub are reported to tolerate a wide range of physicochemical factors and occupy a variety of habitats (Sigler and Sigler 1987, Wilson 1996, Wilson and Belk 1996). Previous studies, however, have focused on leatherside chub habitat use in streams with low densities of brown trout (Wilson 1996, Wilson and Belk 1996). Brown trout are more piscivorous than other salmonids (Sigler and Miller 1963, Minckley 1973) and where introduced are reported to cause a decrease in native fish populations (McDowall 1968, Moyle 1976, Garman and Nielsen 1982).

Past studies have shown that in the presence of fish predators, small stream fishes select shallower habitats with increased structural complexity (Cerri and Fraser 1983, Power et al. 1985, Schlosser 1987). Mittelbach (1981) showed that in the presence of largemouth bass (*Micropterus salmoides*), small bluegill sunfish (*Lepomis macrochirus*) balance their net energetic intake against the cost of predation by foraging in less productive but safer littoral habitats. Large bluegill sunfish, which are less vulnerable to predation, feed in open water and maximize their energetic return. Power (1984) reported that armored catfish (Loricariidae) avoid shallow habitats in the presence of predatory birds. These studies suggest that patterns of habitat choice observed among stream fishes are partially a result of predation.

The objectives of this study were to (1) examine the distribution and habitat use of leatherside chub in a system with high densities of brown trout, and (2) compare results with published accounts of leatherside chub habitat use in streams with few or no brown trout. Because previous investigators (Cerri and Fraser 1983, Schlosser 1987) have shown that predation can influence habitat choice in stream fishes, we predicted that habitat use of

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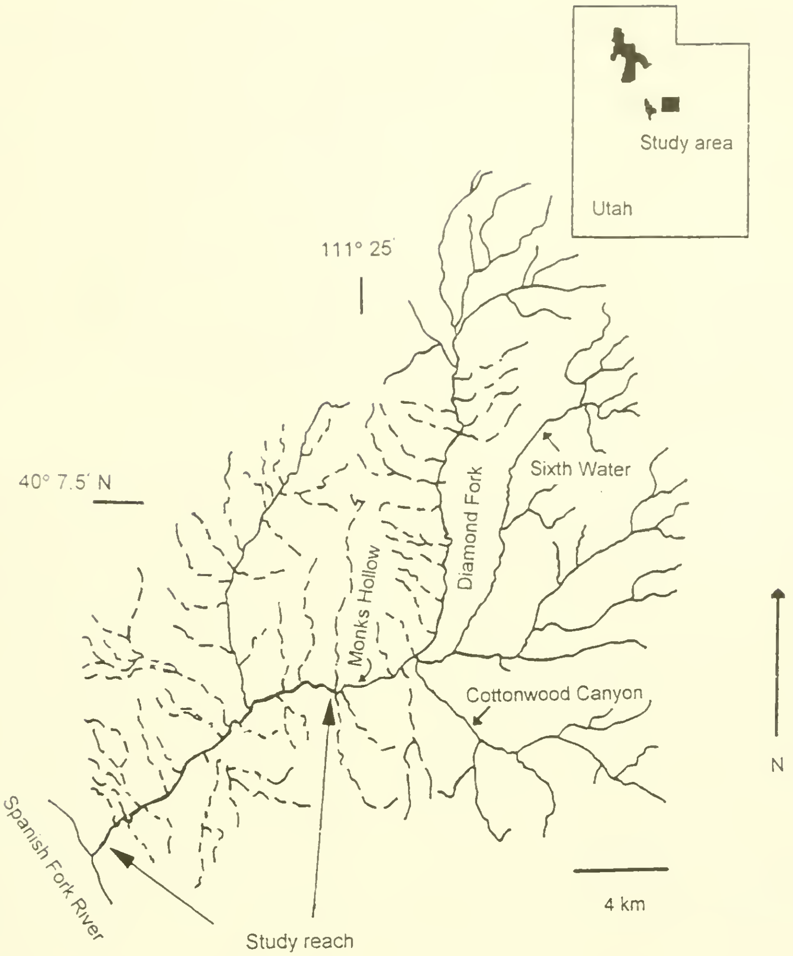

Fig. 1. Map of Diamond Fork Creek, Utah, showing study reach. Dashed lines represent intermittent streams.

leatherside chub in a system dominated by brown trout would differ from habitat use in streams with few or no brown trout (Wilson and Belk 1996). Conclusions could have important implications regarding conservation of leatherside chub, especially in areas managed for brown trout sport fisheries.

MATERIALS AND METHODS

We obtained data on leatherside chub distribution and habitat use from a 14-km section of Diamond Fork Creek (40°7.5′N, 111°25′W), a 4th-order tributary to the Spanish Fork River in north central Utah. Diamond Fork Creek supports a well-established brown trout fishery with a 1997 population estimate of 324 brown trout per km (Charlie Thompson, fisheries biologist, Utah Division of Wildlife Resources, Central Division, personal communication). Our study area extended from approximately 0.5 km above Diamond Fork's confluence with the Spanish Fork River (elevation 1500 m) to Monks Hollow (Fig. 1). Average daily discharges in the mainstem Diamond Fork range from 0.95 m^3s^{-1} during October and November to 12.90 m^3s^{-1} from late June to early August (USGS Gaging Station records). High summer flows are the result of irrigation water transfers from Strawberry River drainage (Colorado River basin) to Diamond Fork Creek drainage (Bonneville River basin).

We surveyed the 14-km study reach in early October 1996 to determine macrohabitat use by leatherside chub. Macrohabitat refers

TABLE 1. Mean, standard deviation (s), and range of microhabitat parameters for 393 lateral (backwater and cutoff pool) habitats in Diamond Fork Creek, Utah.

Habitat variable	Mean	s	Range
Length (m)	8.7	9.4	0.7–72.0
Width (m)	2.1	1.5	0.3–15.0
Surface area (m^2)	25.2	57.1	0.2–900.0
Depth (cm)	24.2	17.6	2.0–100.0
Substrate*	1.4	0.97	1–7
Silt*	1.9	0.9	0–3
Current*	1.0	0.9	0–3
Cover (% surface area)	18.2	22.9	0–100
Number of brown trout	0.6	1.6	0–10
Overhanging vegetation (% surface area)	1.7	7.1	0–50

*Variables treated categorically (refer to Materials and Methods)

Substrate: 1 = silt, 2 = sand, 3 = gravel, 4 = gravel/cobble mix, 5 = gravel/sand mix, 6 = cobble/sand mix, 7 = boulder

Silt. 0 = absent, 1 = slight, 2 = moderate, 3 = heavy

Current. 0 = absent, 1 = slow, 2 = moderate, 3 = fast

to general features (e.g., riffle, pool, backwater) found throughout a stream reach. Macrohabitats were classified as main channel (pool, riffles, and runs within the main channel) or lateral (cutoff pools and backwaters). At the time of investigation, cutoff pools were isolated from the main channel and typically contained moderate to high levels of sediment. Backwaters also were prone to sediment accumulation but were connected to the main channel. Because of their overall slower current, lateral habitats generally contained greater amounts of cover (e.g., vegetation, brush) than main channel habitats. Main channel riffles and runs were dominated by gravel and cobble substrates. Depositional pools, well represented in the main channel, often were associated with instream structures (e.g., boulders, logs).

Moving upstream, we systematically sampled all definitive macrohabitats (sites) within the 14-km reach. We encountered approximately 20 macrohabitats per 0.5 km of stream and sampled with a backpack electrofisher 500 sites equally distributed between main channel and lateral habitats. Electroshocking is efficient for sampling fish near cover such as vegetation, logs, and undercut banks, and over rock substrates in fast currents (Vadas 1991). Each site was shocked for 10 sec at 200 volts to minimize harmful effects on fish. Via previous experimentation, we determined that 10 sec was sufficient to obtain a representative sample. Presence or absence of leatherside chub at each site was recorded.

Subsequent sampling in late October and early November 1996 focused on microhabitat use (e.g., substrate type, current, cover characteristics, etc.) of leatherside chub in lateral habitats. Microhabitat refers to characteristics of habitat experienced by individual leatherside chub within the stream (1- to 3-m radius around the focal area). Sampling upstream, we surveyed 393 lateral habitats throughout the 14-km study reach. Lateral habitats had an average surface area and water depth of 25.2 m^2 and 24.2 cm, respectively (Table 1). Distances between sites ranged from 0.5 m to 125 m. Each site was shocked for 10 sec at 200 volts and the number of leatherside chub and brown trout was recorded. Using a meter stick, we measured maximum water depth, habitat length, and maximum habitat width at each site. Length and width were used to calculate habitat surface area. Current, depth, substrate, silt, cover, and overhanging vegetation were visually estimated at each site. Current was categorized as absent, slow, moderate, or fast. Dominant substrate type was characterized as silt (<2.50 mm), sand (2.50–6.24 mm), gravel (6.25–74 mm), cobble (75–299 mm), and boulders (>300 mm). Cover was recorded as percent of surface area in root, algae, vegetation, brush, leaf litter, and log. Silt coverage (percent of surface area) was categorized as absent (0%), slight (1–25%), moderate (26–50%), or heavy (>50%). Overhanging vegetation was recorded as percent of surface area. We used logistic regression (LOGIST procedure; SAS 1988) to test (1) associations among microhabitat variables and presence of leatherside chub, (2) the relationship between presence of leatherside chub and number of brown trout, and (3) differences in microhabitat between sites where leatherside chub and brown trout co-occurred and sites with only leatherside chub.

RESULTS

Macrohabitat

A single leatherside chub was found among 250 main channel sites sampled. Leatherside chub were present in 49 of 250 (19.6%) lateral sites. Leatherside chub were most common in downstream reaches (<8 km above the mouth) of Diamond Fork Creek (Fig. 2). Overall, the downstream channel was more braided and contained abundant lateral habitat. Leatherside chub were rare in the highly channelized upstream (≥8 km above the mouth) reaches (Fig. 2).

Microhabitat

We encountered 870 leatherside chub in 72 of 393 (18.3%) lateral habitats. We found a significant positive association between presence of leatherside chub and habitat depth ($\chi^2 = 18.21$, $P = 0.0001$, $n = 393$). Silt coverage was also an important predictor of leatherside chub presence ($\chi^2 = 12.51$, $P = 0.0004$, $n = 393$), with most fish favoring depositional habitats with heavy silt (Fig. 3). Leatherside chub also tended to be less abundant in fast currents ($\chi^2 = 3.45$, $P = 0.06$, $n = 393$; Fig. 3). No other physical habitat parameter was significantly associated with presence of leatherside chub.

We found presence of leatherside chub to be significantly negatively associated with number of brown trout ($\chi^2 = 4.07$, $P = 0.04$, $n = 393$). The 2 species co-occurred in 9 of 126 sites (7%) where either species was found. We found no significant differences in microhabitat structure between sites where leatherside chub and brown trout co-occurred and sites with only leatherside chub ($n = 9$ and $n = 63$, $P > 0.30$, respectively). We did not measure size of leatherside chub, although lengths appeared to be within the range reported by Johnson et al. (1995) for Thistle Creek (5 km south of Diamond Fork Creek). We observed no obvious differences in size between leatherside chub found with brown trout and those found alone.

DISCUSSION

Leatherside chub in Diamond Fork Creek were most abundant in deep, low-flow habitats with heavy silt (Fig. 3). A significant positive relationship between leatherside chub and silt suggests a preference for depositional areas. In Salina Creek, a 3rd-order tributary of the Sevier River, Wilson (1996) found leatherside chub to be more abundant in deeper water with lower velocities. However, in contrast to our findings, Wilson (1996) reported that leatherside chub in Salina Creek preferred habitats with less silt.

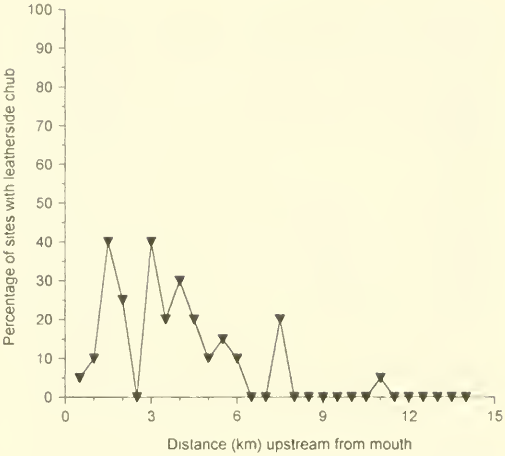

Fig. 2. Percentage of macrohabitat sites in Diamond Fork Creek, Utah, containing *Gila copei* in relation to distance (km) upstream from mouth. On average, 20 sites were sampled per 0.5 km of stream.

The absence of leatherside chub from main channel habitats in Diamond Fork Creek is inconsistent with their habitat use in other systems. Throughout their range, leatherside chub are reported to occupy main channel riffle and pool habitats (Sigler and Sigler 1987, Wilson 1996), where they feed on small aquatic insects in the drift (Sigler and Sigler 1987). Wilson (1996) found 111 leatherside chub in a 100-m reach of main channel in Salina Creek, which is similar to Diamond Fork Creek in size, elevation, and gradient, but supports low densities of brown trout. Wilson (1996) collected no brown trout in a 100-m reach of Salina Creek.

Differences in chub habitat use between systems with and without brown trout and a negative association we observed between leatherside chub and brown trout indicate that brown trout predation may be an important factor affecting chub habitat use. Two pieces of evidence support the predation hypothesis. First, while suitable microhabitats (e.g., depositional habitats downstream of boulders and logs) were well represented in the main channel of Diamond Fork, these habitats contained

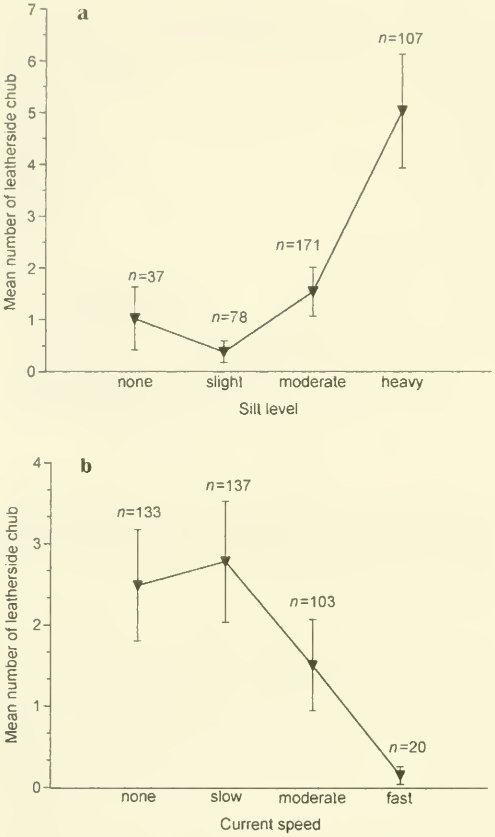

Fig. 3. Mean number of *Gila copei* (±1 $s_{\bar{x}}$, n = 393) encountered at different (a) silt levels and (b) current speeds in Diamond Fork Creek, Utah.

no leatherside chub but often supported brown trout. Second, leatherside chub were uncommon in upstream reaches of Diamond Fork Creek where lateral habitats were rare (Fig. 2). Because the upstream reaches of Diamond Fork were similar in physiography to Salina Creek (where leatherside chub are abundant), we would expect main channel habitats of Diamond Fork to be suitable for leatherside chub.

Our data suggest that brown trout predation in Diamond Fork Creek limits leatherside chub to lateral habitats (areas of low flow and heavy silt). Brown and Moyle (1991) found that introducing Sacramento squawfish (*Ptychocheilus grandis*), a major predator, into the Eel River, California, resulted in changes in habitats occupied by resident fishes. Schlosser (1987) reported that habitat use by warmwater stream fishes was related to presence of predatory centrarchids.

Brown trout have the potential to extirpate other fish from entire stretches of stream (McDowall 1968, Moyle 1976, Garman and Nielsen 1982, Waters 1983). Low-diversity systems with few native predators (like Diamond Fork Creek) are reported to be especially sensitive to effects of introduced predators (Johaness and Larkin 1961, McDowall 1968, Christie et al. 1972, Ross 1991). Even though leatherside chub co-evolved with predatory cutthroat trout (*Salmo clarki;* Sigler and Miller 1963), stream-dwelling cutthroat trout are reported to feed exclusively on aquatic invertebrates (May et al. 1978) and probably do not pose the same predatory "threat" to leatherside chub as do brown trout. Thus, leatherside chub may be especially sensitive to brown trout predation because the chub evolved in the absence of a highly piscivorous predator.

In light of our findings, recent changes in the management of summer flows and new regulations concerning the brown trout fishery could have serious effects on long-term survival of leatherside chub populations in Diamond Fork. High summer flows in Diamond Fork Creek are due to diversion of water from the Colorado River basin into the Bonneville River basin. The diversion, for summer irrigation demands, delivers up to 14 m^3s^{-1} of water to Sixth Water Creek in Diamond Fork Creek drainage (Fig. 1). In 1996 construction began on a pipeline to transfer water from Sixth Water Creek directly into the Spanish Fork River, bypassing lower Diamond Fork Creek. Once operational, the pipeline will return flows in Diamond Fork Creek to near pre-transfer levels. Currently, high summer flows in Diamond Fork form lateral habitats by flooding low-lying areas. High flows allow many of these habitats to persist during dry summer months and may aid in survival of juvenile leatherside chub. Sigler and Sigler (1987) reported that young leatherside chub often seek low-flow areas close to shore. Reduction of summer flows to pre-transfer levels potentially could reduce abundance and persistence of these habitats. Without adequate lateral habitats, leatherside chub could be forced into the main channel where the risk of predation by brown trout is greater.

Potential changes in brown trout fishery management in Diamond Fork also may have a negative impact on leatherside chub. Catch-and-release regulations have been implemented upstream of the study site, and such regulations typically shift size structure toward larger classes. Because large brown trout are reported to be more piscivorous than small ones (Wiley 1978, Garman and Nielsen 1982), we predict that implementation of a catch-and-release fishery in Diamond Fork could have a serious negative impact on persistence of leatherside chub.

Our data suggest that lateral habitats may serve as refugia for leatherside chub against brown trout predation. While predation seems to be an important factor affecting habitat use by leatherside chub, more detailed experimental investigations are required to adequately examine the interactions between brown trout and leatherside chub. Restoration efforts aimed at preserving leatherside chub in an established brown trout fishery should concentrate on maintaining lateral habitats. Careful consideration should be given to introduction of brown trout to streams with leatherside chub, especially if these systems contain little lateral habitat.

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CHEEK POUCH CAPACITIES AND LOADING RATES OF DEER MICE (*PEROMYSCUS MANICULATUS*)

Stephen B. Vander Wall[1] and William S. Longland[2]

ABSTRACT.—Eight deer mice (*Peromyscus maniculatus*) were attracted to bait stations in the field and filled their cheek pouches with seeds. Pouch capacity of the deer mice, which have small, internal cheek pouches, was 0.45 ± 0.11 mL, about 12–27% of that carried by similar-sized heteromyid rodents. Cheek pouches of deer mice, although small, give them the capacity to carry 3–5 times more food than unspecialized mice. This presumably increases efficiency of deer mice in exploiting small, particulate food items that are patchily distributed.

Key words: food transport, granivory, seed harvesting, Heteromyidae, Indian ricegrass, Muridae.

In 1942 W.J. Hamilton described deer mouse (*Peromyscus maniculatus*) internal cheek pouches. Since that time little has been written about these structures. To understand the role of cheek pouches in the foraging economics of deer mice, it is first necessary to know pouch size. For instance, knowledge of load sizes of food items that can be carried during foraging may help us understand how deer mice exploit resources within their home range. During a study of cheek pouch size of the Heteromyidae (Vander Wall et al. 1998), we had the opportunity to gather data on load sizes of 8 deer mice. Here we describe the loads carried by these rodents and compare them to loads carried by pocket mice and kangaroo rats, species known for their well-developed, external cheek pouches.

STUDY AREA

We collected most field data on deer mice along Red Rock Road, 20–26 km north of Reno, Washoe County, Nevada. Habitat in this area consists of burned and unburned shrubs (mostly sagebrush, *Artemisia tridentata*) with grasses and scattered junipers (*Juniperus osteosperma*). Data on 1 subject were collected in open, rocky grassland habitat in the Lake Range ≈24 km south of Empire, Washoe County, Nevada. We conducted laboratory procedures at the Department of Biology, University of Nevada, and the United States Department of Agriculture, Agricultural Research Service in Reno, Nevada.

METHODS

Our field methods are described in detail in Vander Wall et al. (1998). We established 10–20 bait stations just before dark using ≈20 g of mixed millet and sunflower seeds and inspected each station at ≈15-min intervals. When a bait station showed evidence of depletion by a rodent, we placed a cafeteria tray containing a thin layer of sand on top of the bait station and poured a preweighed quantity of unhusked Indian ricegrass (*Oryzopsis hymenoides*) seeds onto the sand. Then we retreated to a distance ≈10 m away and watched with night-vision goggles. When a rodent returned, we timed seed loading (time in contact with the seed pile) with a stopwatch. After the subject departed, we replaced the cafeteria tray with an identical one, poured a new batch of preweighed seeds onto the sand, and retreated. While we waited for the subject to return, we placed the 1st sample in a plastic bag for later analysis. By repeating this sequence 2–6 times we obtained a series of separate estimates of load size. After the final load, we trapped the subject using a single trap placed at the bait station. The subject's sex and mass were recorded and its species confirmed. Identity of the subject was based on its consistent, goal-oriented behavior as it approached the bait station or trap. If we suspected that more than 1 individual was visiting a bait station, we terminated that trial and moved to a new site. We gathered field data

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TABLE 1. Body mass, cheek pouch capacities, loading rates, and mean loading times for 8 deer mice that loaded their cheek pouches with Indian ricegrass seeds. Two subjects were not captured to determine sex and body mass. *N* refers to number of times each subject filled its cheek pouches.

Sex	Body mass (g)	Pouch capacity (mL)			Loading rate (seed/sec)			Mean loading time (sec)
		N	Max	Mean ± *s*	*N*	Max	Mean ± *s*	
M	16	6	0.53	0.48 ± 0.06	—	—	—	—
F	14	3	0.39	0.31 ± 0.12	3	3.0	2.9 ± 0.7	21
F	13	3	0.44	0.41 ± 0.03	2	2.2	2.1 ± 0.1	35
M	19	3	0.56	0.52 ± 0.04	3	3.4	3.2 ± 0.3	28
F	13	4	0.61	0.51 ± 0.09	4	4.5	3.6 ± 0.6	25
M	16	3	0.36	0.27 ± 0.10	3	2.2	1.8 ± 0.3	25
—	—	2	0.49	0.46 ± 0.05	2	2.9	2.9 ± 0.0	27
—	—	3	0.69	0.60 ± 0.12	3	5.6	4.6 ± 0.9	22

on deer mice between 16 May and 25 July 1994 and on 7 July 1996.

In the laboratory we recovered seeds from the bagged sample by sifting them from the sand. *Load* was operationally defined to mean the quantity of seeds held in the cheek pouches and *capacity* the volume of cheek pouches when filled with seeds. We calculated load mass by subtracting mass of recovered seeds from mass of those originally offered, and then converted mass to pouch capacity by dividing by bulk density (which includes air spaces between seeds) of Indian ricegrass seeds (0.70 g/mL). We calculated seed loading rates by counting the number of seeds in a gram (mean of 245 for unhusked Indian ricegrass), multiplying by the number of grams per load, and dividing by the number of seconds taken to fill the cheek pouches.

RESULTS

Eight deer mice took seeds from bait stations, and we were able to capture 6 of these to determine their body mass and sex and to confirm species. Three were males and 3 females (Table 1). Mean cheek pouch capacity of the 8 subjects was 0.45 ± 0.11 mL. Mean load size was equivalent to 76 ± 19 Indian ricegrass seeds. We compared pouch capacities of 6 captured subjects to theoretical heteromyids of the same body mass (Fig. 1) using the allometric relationship

$$\text{capacity (mL)} = 0.148\text{bodymass(g)}^{0.992}$$

which relates pouch capacity to body mass of heteromyid rodents (Vander Wall et al. 1998). Deer mice pouch capacities ranged from 12% to 27% (mean = 19%) of that carried by equal-sized heteromyids.

Loading time of deer mice averaged 26 ± 5 sec (n = 20 loads), and mean loading rate was 3.0 ± 0.9 seeds/sec (n = 7 subjects). These rates were 17–40% of the loading rates for similar-sized heteromyids (Vander Wall et al. 1998).

DISCUSSION

Deer mice apparently use their cheek pouches to accumulate seeds and perhaps other food items as they forage. These mice routinely forage 50–100 m from their burrows and often travel much farther to rich sources of food (e.g., Criddle 1950). They then either scatter hoard seeds in the soil (Vander Wall 1997, unpublished data) or transport them back to their burrows, where they eat them or add them to their larders (Criddle 1950, Howard and Evans 1961, Barry 1976, Tadlock and Klein 1979). But compared to heteromyids, deer mice carry small seed loads (Fig. 1). Hamilton (1942), when he first described cheek pouches of deer mouse, reported 13 jewel weed (*Impatiens capensis*) seeds being carried by 1 individual. Cogshall (1928) found that deer mice could carry about 10 wheat kernels. Abbott and Quink (1970) found that typical caches of eastern white pine (*Pinus strobus*) seeds (≈15 mg/seed) made by white-footed mice (*Peromyscus leucopus*) contained 20–30 seeds, the largest caches probably representing capacity loads. But despite the relatively small size of their cheek pouches, deer mice are able to accumulate a liter or more of seeds in their nest burrows (Criddle 1950, Howard and Evans 1961, J.C. Chambers personal communication). Larders of this size must represent thousands of trips made by individuals.

By comparing load sizes of deer mice to those of unspecialized rodents, it is possible to

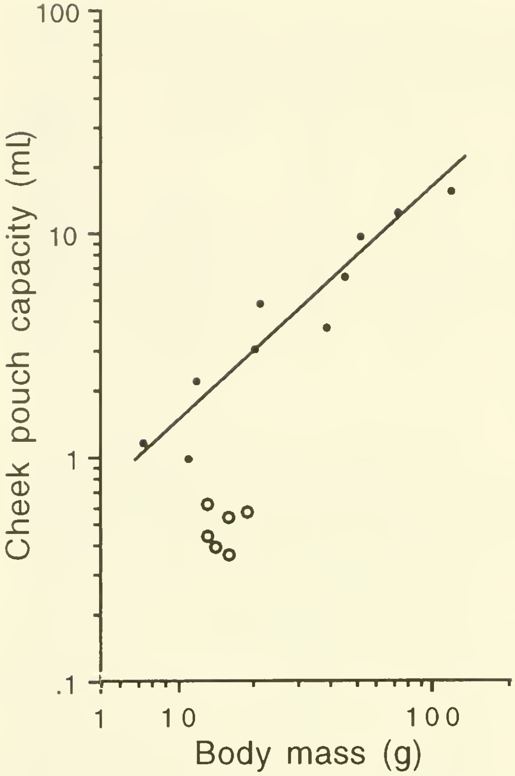

Fig. 1. The relationship between body mass and cheek pouch capacity for 6 deer mice (open circles) on a double logarithmic scale. The regression line (filled circles) is the allometric relationship for 10 heteromyid rodent species: capacity (mL) = 0.148bodymass(g)$^{0.992}$, r^2 = .91, df = 9, P < .0001 (Vander Wall et al. 1998).

gain some insight into benefits that cheek pouches confer upon deer mice. We were unable to find any reports of load sizes transported by rodents that lack cheek pouches, but a 36-g northern grasshopper mouse (*Onychomys leucogaster*) that made 2 visits to 1 of our seed trays carried away only 0.26 and 0.11 mL. Grasshopper mice are generally insectivorous and carnivorous and apparently lack specialized cheek pouches. They are known to gather seeds and other items and store them for later use (Ruffer 1965, McCarty and Southwick 1975). After making adjustments for differences in body mass, deer mice carry between 3 and 5 times as much food in their cheek pouches as did the northern grasshopper mouse. Although deer mice are not nearly as efficient at transporting foods as are heteromyids, they are considerably more efficient than rodents that lack cheek pouches. The ability of deer mice to transport small loads of food presumably increases their efficiency in exploiting small, particulate food items that are patchily distributed.

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ECOLOGICAL IMPACTS OF *POGONOMYRMEX* ON WOODY VEGETATION OF A *LARREA-AMBROSIA* SHRUBLAND

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Abstract.—Plant species richness, density, and frequency were quantitatively examined within *Pogonomyrmex rugosus* (seed-harvester ant) nest discs and at various distances from nest discs in a *Larrea tridentata–Ambrosia dumosa* (creosote bush–white bursage) shrubland in southern Nevada. Woody vegetation at and near the edge (perimeter) of nest discs showed decreased species richness, density, and frequency compared with vegetation in adjacent reference areas (nonnest: 4 m beyond discs). Four of 17 species were found with significantly lower density and frequency on nest discs than at greater distances from the nest. Thirteen of 17 species were not found on nest discs at all. Species richness, density, and frequency were significantly and negatively correlated with distance from nests. Woody vegetation was sparse and less variable in composition when occurring at discs and edges of discs. Local disturbances caused by *P. rugosus* nests may largely alter immediate surrounding vegetation in the *L. tridentata–A. dumosa* shrubland of southern Nevada.

Key words: Pogonomyrmex rugosus, *woody vegetation, nest, colony, disc, edge,* Larrea tridentata, Ambrosia dumosa, *southern Nevada.*

Pogonomyrmex rugosus (seed-harvester ant) occurs in arid and semiarid plant communities throughout much of southwestern United States (Carlson and Whitford 1991). Previous studies have shown that ant activities can change vegetation patterns and composition (Beattie and Culver 1977, Culver and Beattie 1983, Hobbs 1985, Rissing 1986, 1988, Carlson and Whitford 1991). Nests of *Pogonomyrmex* species are generally clear of plants at least in the central area surrounding the single nest entrance where ant activities are most intense (Beattie and Culver 1977). Because ant colonies are usually overdispersed, associated vegetation appears to be patchy and variable in composition (Beattie and Culver 1977). Most mounds in the Mojave Desert of southern Nevada and in the Sonoran Desert of central Arizona often have been cleared completely or almost completely of vegetation by the ants (Rissing 1986, 1988). Similarly, other studies have found changes in plant diversity and composition (Beattie and Culver 1977, Culver and Beattie 1983), population densities (Hobbs 1985), and vegetation production (Rogers and Lavigne 1974) associated with ant nests. A study in New Mexico (Carlson and Whitford 1991) has shown that *Pogonomyrmex* species also may alter vegetation by soil modification, destruction of plants, seed dispersal, and/or seed predation.

Larrea tridentata–Ambrosia dumosa (creosote bush–white bursage) is a dominant vegetation type in southern Nevada, and yet ecological impacts of *P. rugosus* on this vegetation type are not fully understood. This article explores ecological impacts of *P. rugosus* nests on plant species richness, density, and frequency by analyzing woody vegetation at varying distances from colonies in the *L. tridentata–A. dumosa* shrubland in southern Nevada.

Methods

Study Site

Field studies were conducted in *L. tridentata–A. dumosa* shrubland in Henderson, near Las Vegas, Nevada (roughly 36°00′N, 115°00′W; elevation 750 m), during spring 1997. Vegetation is composed predominantly of *L. tridentata* and *A. dumosa* with scattered distribution of other woody taxa, including *Krameria parvifolia* (ratany), *Ephedra nevadensis* (Nevada ephedra), *Eurotia lanata* (winterfat), and *Yucca schidigera* (Mojave yucca). Soils, derived from limestone-dolomite mountains and hills, are sandy in texture with loose rocks on the surface.

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Climate and vegetation in southern Nevada are typical of the eastern Mojave Desert. Summer air temperatures often surpass 35°C, and winter temperatures rarely fall below freezing. Annual precipitation ranges from trace amounts to approximately 110 mm, increasing with altitude in the higher mountains (Bradley and Deacon 1967). Most annual precipitation occurs in winter storms and in summer monsoonal thunderstorms; relative humidity of ≤20% is common in summer months (Lei and Walker 1997).

Field Surveys

Potential impacts of *P. rugosus* on vegetation of the *L. tridentata–A. dumosa* shrubland were investigated by identifying and counting all plants growing within 4 m from the perimeter of the cleared areas of *P. rugosus* nests. Three hundred forty-nine (349) *P. rugosus* nests located on a 15-ha site were sampled for the vegetation study. Five 0.5-m^2 (50 × 100-cm) quadrats were established per colony. Quadrat placement was in a random compass direction from each colony. Within each quadrat, plant species composition and density were determined for each nest: disc, immediately adjacent to the disc (edge), 1.0, 2.0, and 4.0 m from the outermost disc edges, with the latter (4 m) serving as a nonnest reference area. Disc quadrats were located approximately midway between the center (nest entrance) and outermost edge (perimeter) of a nest. Plant species richness (number of species per quadrat), density (number of individuals per 0.5 m^2), and frequency (number of plots in which a plant species was found) were computed and compared with varying distances from *P. rugosus* nests. Density of nests per hectare was determined by counting nests and dividing by the total site area.

Statistical Analyses

One-way analysis of variance (ANOVA), followed by Tukey's multiple comparison test, was used (1) to detect differences in plant species richness, density, and frequency at various distances from *P. rugosus* nests, and (2) to compare site means when a significant distance effect was detected (Analytical Software 1994). Mean values of species richness are expressed with standard errors, and statistical significance was determined at $P \leq 0.05$.

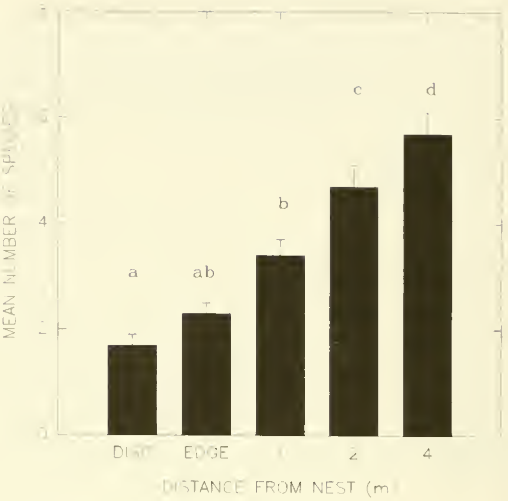

Fig. 1. Mean species richness of woody vegetation sampled in 0.5-m^2 quadrats within *P. rugosus* nest discs and at various distances from discs in the *L. tridentata–A. dumosa* shrubland (n = 349). Narrow vertical bars represent standard errors, and different letters at column tops indicate significant differences at $P \leq 0.05$.

RESULTS

Pogonomyrmex rugosus had local effects on immediate surrounding vegetation in the *L. tridentata–A. dumosa* shrubland. Density of *P. rugosus* reached 23.3 colonies per hectare. Seventeen woody plant species were found in this study. Species richness declined significantly ($P \leq 0.001$; Fig. 1) when approaching *P. rugosus* colonies. Bare ground was observed at the center and disc perimeter of most *P. rugosus* nests. Four of 17 woody species were found at significantly lower density and frequency on nest discs than at greater distances from ant nests (Tables 1, 2). *Larrea tridentata* showed highest density and frequency among all woody taxa on nest discs (Tables 1, 2). However, 13 of 17 species did not exist at all on nest discs (Tables 1, 2). *Opuntia acanthocarpa* (buckhorn cholla), *O. basilaris* (beavertail), *O. echinocarpa* (silver cholla), and *O. ramosissima* (pencil cholla) occurred ≥1 m from *P. rugosus* nests (Table 1).

Significant negative correlations were detected between species richness and distance

TABLE 1. Mean density of woody species sampled in 0.5-m^2 quadrats within *P. rugosus* nest discs and at various distances from discs in the *L. tridentata–A. dumosa* shrubland (n = 349). Mean values in rows followed by different letters are significantly different at $P \leq 0.05$.

	Distance from disc (m)				
Species	Disc	Edge	1	2	4
Acamptopappus shockleyi	0a	0.02ab	0.04b	0.10c	0.23d
Ambrosia dumosa	0.08a	0.12ab	0.14b	0.25c	0.44d
Encelia virginensis	0a	0.03b	0.02b	0.09c	0.15d
Ephedra nevadensis	0a	0.04b	0.13c	0.19cd	0.32d
Eriogonum fasciculatum	0a	0.03b	0.04b	0.08bc	0.13c
Eurotia lanata	0	0.04b	0.04b	0.06b	0.14c
Hymenoclea salsola	0.04a	0.05a	0.11b	0.17c	0.17c
Krameria parvifolia	0.08a	0.11a	0.20b	0.20b	0.28c
Larrea tridentata	0.12a	0.22b	0.30b	0.54c	0.64d
Opuntia acanthocarpa	0a	0a	0.01b	0.01b	0.08c
Opuntia basilaris	0a	0a	0.02b	0.03b	0.03b
Opuntia echinocarpa	0a	0a	0.01b	0.01b	0.03b
Opuntia ramosissima	0a	0a	0.02b	0.01b	0.02b
Psorothamnus fremontii	0a	0a	0.03b	0.02b	0.05c
Salazaria mexicana	0a	0a	0.02b	0.01b	0.03b
Stephanomeria pauciflora	0a	0.02b	0.02b	0.04bc	0.06c
Yucca schidigera	0a	0.01b	0.01b	0.05c	0.14d

TABLE 2. Mean frequency of woody species sampled in 0.5-m^2 quadrats within *P. rugosus* nest discs and at various distances from discs in the *L. tridentata–A. dumosa* shrubland (n = 349). Mean values in rows followed by different letters are significantly different at $P \leq 0.05$.

	Distance from disc (m)				
Species	Disc	Edge	1	2	4
Acamptopappus shockleyi	0a	4.6b	9.5bc	14.0c	17.2c
Ambrosia dumosa	12.3a	25.5b	41.2c	54.1d	57.3d
Encelia virginensis	0a	1.8b	2.3b	4.6c	7.7c
Ephedra nevadensis	0a	2.9b	4.9b	25.5c	31.8c
Eriogonum fasiculatum	0a	1.8b	2.9b	4.4bc	5.9c
Eurotia lanata	0a	2.9b	3.7b	6.3bc	8.3c
Hymenoclea salsola	5.4a	6.9a	8.3a	11.2ab	15.7b
Krameria parvifolia	6.9a	11.2b	18.9c	28.3d	31.5d
Larrea tridentata	16.3a	19.2a	28.6b	31.5b	63.6c
Opuntia acanthocarpa	0a	0a	1.7b	4.3bc	7.2c
Opuntia basilaris	0a	0a	2.6b	4.5bc	7.2c
Opuntia echinocarpa	0a	0a	3.4b	3.7b	5.7c
Opuntia ramosissima	0a	0a	2.3b	2.6b	5.4c
Psorothamnus fremontii	0a	0a	4.0b	4.6b	8.3c
Salazaria mexicana	0a	0a	4.9b	6.3b	11.1c
Stephanomeria pauciflora	0a	2.8b	4.9b	4.6b	8.9c
Yucca schidigera	0a	0.9b	0.9b	9.2c	28.7d

from *P. rugosus* nests ($r = -0.49$, $P \leq 0.001$), between species density and distance from nests ($r = -0.58$, $P \leq 0.001$), and between species frequency and distance from nests ($r = -0.68$, $P \leq 0.001$). Flora within and around disc perimeters was relatively homogeneous (Table 1). On the contrary, flora in adjacent reference areas was significantly more diverse ($P \leq 0.001$; Table 1).

DISCUSSION

Pogonomyrmex rugosus locally influences plants beyond denuded areas as evidenced by decreased species richness, density, and frequency, as well as altered vegetation composition adjacent to discs. Nest discs were generally clear of plants, and local disturbances caused by *P. rugosus* appear to increase vegetation homogeneity, especially within discs and around disc perimeters, in the *L. tridentata–A. dumosa* shrubland. Clark and Comanor (1975) state that the majority of harvester ant species in the genus *Pogonomyrmex* may actively defoliate leaves and destroy plants growing on and near their nests to reduce shade because high nest temperatures are required for brood development.

Species diversity, as well as density, and frequency of some species between disc and edge quadrats and between edge quadrats and 1-cm from edge quadrats were not significantly different. The disc is a visually obvious nest structure, but not the limits of the nest itself, which may extend below the soil surface at a distance beyond the disc. Furthermore, the *P. rugosus* colony influences soil surface beyond the limits or physical structure of the nest disc as well. Perhaps the edge is an interface between the distinct zones of the nest disc and beyond it.

The presence of *P. rugosus* has potential to alter soil properties and to determine germination and reproductive success of woody species, which may ultimately change the successional progression of *L. tridentata–A. dumosa* shrublands. Further investigations are required to examine how patterns of colony abandonment and reestablishment affect a large percentage of the area and influence patterns of soil development and plant community succession through time in southern Nevada.

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NEW RECORDS AND HABITAT INFORMATION FOR *SOREX MERRIAMI* IN NEBRASKA

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ABSTRACT.—We report the collection of 8 additional specimens of *Sorex merriami* from northwestern Nebraska; previously only 2 specimens had been collected in the state. The new specimens were captured in pitfall traps and Sherman live-traps from 1979 through 1996 in Dawes, Sheridan, and Sioux counties. These individuals were caught together with *Sorex cinereus* and several rodent species in a variety of grassland habitats, including disturbed roadsides dominated by native and introduced grasses and forbs, grassland openings in forests of ponderosa pine, and an open, dry grassland. Seven of the new specimens, captured in late May, early June, and December, were young-of-the-year, and 4 of these were not in reproductive condition; reproductive status of the other 3 was not assessed. One individual, captured in late May, was an old male in reproductive condition.

Key words: Sorex merriami, *Nebraska, habitat use, reproduction.*

Distribution of *Sorex merriami* is centered on the Great Basin and extends over a large portion of west central United States, from south central Arizona to northern Montana, and from western Nebraska to central California (Diersing and Hoffmeister 1977, Hall 1981). This species is poorly understood on the Great Plains and was believed to be rare in Nebraska, previously known from only 2 specimens from the northwestern corner of the state (McDaniel 1967, Freeman et al. 1993). The 1st individual was captured in 1965 on the edge of a wet meadow, 4.8 km S Rushville, Sheridan County, in the Niobrara River drainage (McDaniel 1967). The 2nd specimen was captured in 1989 in the White River drainage, 16.1 km N, 12.9 km W Harrison, Sioux County (Freeman et al. 1993). Habitat at this site was dominated by 2 species of *Artemisia*, *Chrysothamnus* sp., and several grass species. Nearby habitats included short-grass prairie and an open forest dominated by *Pinus ponderosa* (Freeman et al. 1993).

NEW SPECIMENS

On the night of 31 May 1979, students from Chadron State College captured a single *Sorex merriami* 30 km S Chadron, Dawes County (T30N, R48W, Sec. 28 NE 1/4 of NW 1/4; housed at University of Nebraska State Museum, UNSM 20921). This animal was caught in a Sherman live-trap in the Niobrara River drainage. Notes on vegetation were not taken at capture, but today this dry grassland is dominated by *Andropogon scoparius*, *Bouteloua gracilis*, *B. curtipendula*, *Calamovilfa longifolia*, *Carex* sp., and scattered forbs. *Artemisia ludoviciana* and *A. frigida* are present, but neither is dominant in the community. Inasmuch as land use at this site has not changed dramatically since 1979, present vegetative conditions are probably similar to those at the time of collection. This female was caught together with *Microtus ochrogaster*, *Peromyscus maniculatus*, and *Perognathus fasciatus* and was not in reproductive condition.

Three *S. merriami* (UNSM 19972–19974) were collected by a field party from Chadron State College at Metcalf Wildlife Management Area, 15 km N Hay Springs, Sheridan County (T33N, R46W, Sec. 24 SW 1/4). These animals were caught in the White River drainage in pitfall traps during the week of 7–13 June 1993. One individual was a male, 1 a female, and the other undetermined. Reproductive condition was not recorded, probably because these specimens were too decomposed. These individuals were caught on a hillside in a grassland opening surrounded by open stands of *Pinus ponderosa*. Vegetation at this site was dominated by native grasses, including

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Andropogon scoparius, Bouteloua hirsuta, B. curtipendula, Calamovilfa longifolia, Stipa sp., and *A. gerardii.* Other dominant plant species included *Yucca glauca, Carex* sp., *Ambrosia artemisifolia,* and *Rhus aromatica.*

Another *Sorex merriami* (UNSM 20927) was captured in a pitfall trap on 24 May 1994 by students from Chadron State College at Gilbert Baker Wildlife Management Area, 8.9 km N, 4 km W Harrison, Sioux County (T32N, R56W, Sec. 8 NW 1/4 of NW 1/4). This animal was captured in the White River drainage in a grassland/shrub opening surrounded by open *Pinus ponderosa* forests. Vegetation on this slope is dominated by *Poa pratensis, Bromus tectorum, Rosa arkansana, Ambrosia psilostachya, Lupinus* sp., and *Yucca glauca.* Scattered clumps of *Artemisia frigida* are present, and the shrew was captured within a large cluster of this shrub. This male was in reproductive condition, based on its enlarged testes (4 × 3 mm), and was captured together with *Peromyscus maniculatus.*

Finally, 3 *Sorex merriami* were collected by one of us (RAB) at 3 different sites in Dawes County on the night of 3–4 December 1996, 40–41 km S Chadron (UNSM 20914, 20917, 20919). The animals were caught in Sherman live-traps in the drainage of the Niobrara River.

The 1st site, where UNSM 20914 was captured (S shoulder Dunlop Road, 6.8 km W Highway 385; T29N, R49W, Sec. 34 NE 1/4), is a moderately steep embankment covered with a mix of *Andropogon scoparius, Bouteloua curtipendula, B. hirsuta, Bromus inermis, Agropyron cristatum, Agropyron smithii, Panicum virgatum, Helianthus petiolaris, Ambrosia artemisifolia,* and *Bromus tectorum.* Three of these species (*Bromus inermis, B. tectorum,* and *Agropyron cristatum*) are introduced. Immediately adjacent to this site is a dry, open grassland, gradually sloping down to the Niobrara River <1 km to the south. This individual was a male with testes measuring 1.5 × 1 mm.

The 2nd site, where UNSM 20917 was captured (S shoulder Dunlop Road, 6 km W Highway 385; T29N, R49W, Sec. 35 NW 1/4), is 0.8 km E of the previous site, has similar vegetation, is located adjacent to the same open grassland, and also is a moderately steep embankment. Both sites are disturbed, roadside shoulder habitat, and grasses appear to have been planted following road construction. This female contained no embryos.

The 3rd site, where UNSM 20919 was captured (E shoulder Highway 385, 2 km S Lembke Road; T29N, R48W, Sec. 28 NW 1/4 of NW 1/4), is a less disturbed site, dominated in part by introduced grasses (*Bromus inermis, B. tectorum,* and *Agropyron cristatum*). Other dominant plants include *Andropogon scoparius, Calamovilfa longifolia, Bouteloua hirsuta, B. curtipendula, Yucca glauca, Helianthus petiolaris,* and *Opuntia* sp. Adjacent to this site are hills covered with native prairie. This individual was a female with no embryos.

The following small mammals were captured with these last 3 *Sorex merriami*: 22 *Microtus ochrogaster,* 16 *Reithrodontomys megalotis,* 1 *R. montanus,* 14 *Peromyscus maniculatus,* and 4 *Sorex cinereus* (120 traps were set at these 3 sites).

Cranial measurements were recorded from the new specimens following Diersing and Hoffmeister (1977). These values (mean [standard error; range], all in mm except where noted), together with the standard external measurements, are as follows: total length 92.62 (1.78; 87–100); length of tail vertebrae 36.12 (1.36; 30–42); length of hind foot 11.86 (0.29; 10.6–13); height of ear 6.71 (0.40; 5–8); mass in grams 3.56 (0.24; 2.7–5); breadth of maxilla 5.09 (0.05; 4.8–5.36); length of skull 15.28 (0.11; 14.64–15.68); breadth of braincase 8.10 (0.08; 7.6–8.48); breadth of upper toothrow 4.80 (0.07; 4.56–5.2); length of upper toothrow 5.96 (0.05; 5.84–6.32); length of complex toothrow 4.18 (0.04; 4–4.4); length of unicuspid toothrow 1.95 (0.03; 1.84–2.08); and breadth of zygomatic plate 1.26 (0.04; 1.04–1.36). Six of 8 new specimens fall within the range of measurements of 102 *Sorex merriami* collected throughout the western United States, reported by Diersing and Hoffmeister (1977). The remaining 2 animals, however, have measurements that fall below these ranges. One individual (UNSM 20921) falls outside the range on 4 characters. Those characters and their values (as well as the range presented in Diersing and Hoffmeister [1977]), all in mm, are as follows: breadth of maxilla 4.80 (4.91–5.62); length of skull 14.64 (14.99–16.57); breadth of braincase 7.60 (7.83–8.92); and breadth of upper toothrows 4.56 (4.65–5.21). Despite its small size, this individual is identified as *Sorex merriami* using keys presented in Jones et al. (1983), Hoffmeister (1986), and Carraway (1995). One other individual reported herein (UNSM 19973) has a hind foot measurement (10.6 mm) less than the range presented by Diersing and Hoffmeister (1977; 11–14 mm). If we compare data from the new specimens only to those shrews reported by Diersing and Hoffmeister (1977) collected on the Great Plains, the shrews presented herein extend the known size range for every measured character except length of upper toothrow.

Age of the new specimens of *Sorex merriami* was estimated by the amount of tooth wear (Churchfield 1990), especially the degree of wear on unicuspids and cusps of the molariform teeth. Four specimens captured in late May/early June have very little to no tooth wear (UNSM 19972–19974, 20921), indicating they are young-of-the-year. Three specimens captured in December 1996 also have light tooth wear (UNSM 20914, 20917, 20919) and were likely born in the spring of that same year. The individual captured in late May 1994 (UNSM 20927) has substantial tooth wear and was probably born in the spring of 1993. This animal is also the only new specimen reported herein that was in reproductive condition. The specimen of *Sorex merriami* collected by Freeman et al. (1993) is very similar to this new specimen in age and sex characteristics; it was captured in June, has enlarged testes, and also has substantial tooth wear.

None of the specimens of *Sorex merriami* reported here was molting. Molt in this species apparently occurs in April and then again in October and November (Jones et al. 1983).

The collection of these specimens of *Sorex merriami* broadens the view of the biology of this species in the Great Plains portion of its geographic range. Their capture extends the known range of the species in the state to the north and south, suggesting that it may be distributed continuously across the northwestern corner of Nebraska. The habitat in which these shrews was captured also is different from that previously described for this species on the Great Plains (McDaniel 1967, Freeman et al. 1993, Mullican 1994). Three of the shrews were captured in disturbed roadside vegetation dominated in part by introduced grasses. Four other specimens were captured in small grassland openings surrounded by open forests of ponderosa pine. The 3 previously reported specimens from the Great Plains were captured in sage/grassland habitats (Freeman et al. 1993, Mullican 1994) or along the edge of a wet meadow (McDaniel 1967). Elsewhere, Merriam's shrews have been captured in association with ponderosa pine and other conifers in Arizona and southern Colorado (Hoffmeister 1956, 1986). In addition, this is the 1st time in Nebraska that several Merriam's shrews have been captured in a short period of time (3 in 1 night in 1 instance), suggesting the species may be more common in the state than previously thought. Finally, this is one of the 1st reports of surface activity of this species in winter conditions. Temperatures reached a low of –6°C during the night that *Sorex merriami* was caught in December 1996.

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HABITAT CHARACTERISTICS OF REPTILES IN PINYON-JUNIPER WOODLAND

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Key words: reptiles, habitat use, pinyon-juniper woodland, Inyo Mountains, White Mountains, California.

The Inyo Mountains and White Mountains rise in elevation from 1515 to 4245 m and are east of, and run parallel to, the Sierra Nevada on the western border of the Great Basin. Pinyon-juniper (*Pinus monophylla–Juniperus osteosperma*) woodland predominates between ca 1800 and 2900 m elevation and is characterized by an increasing concentration of pinyon and a decreasing amount of juniper with increased elevation. The shrub layer is sparse and composed primarily of sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia glandulosa* and *P. tridentata*), intermixed with Mormon tea (*Ephedra viridis*), rabbitbrush (*Chrysothamnus nauseosus* and *C. viscidiflorus*), cactus (*Opuntia* and *Echinocereus* spp.), and other less common grasses and herbaceous plants. A thorough description of the environment and flora of these ranges was given by Powell and Klieforth (1991) and Spira (1991).

Only a few studies have documented distribution and habitat affinities of amphibians and reptiles in the pinyon-juniper zone of these ranges (Macey and Papenfuss 1991a, 1991b, Morrison and Hall in press). Pinyon-juniper woodlands are impacted by numerous activities that alter habitat, including grazing and fuelwood harvesting. Better quantification of fauna in these areas is necessary before resource professionals can develop management plans that adequately consider herpetofauna. In this paper we describe a 3-yr study of abundance and habitat characteristics of lizards in a pinyon-juniper woodland. Our objectives included determining interspecific relationships in abundance and correlation between abundance and habitat conditions.

We established 3 trapping grids to intensively sample the pinyon-juniper zone: "Pinyon" (T7S, R35E, sec. 29) and "Cedar" (T7S, R35E, sec. 32) were about 1.5 km apart, and "Westgard" (T8S, R35E, sec. 9) was about 7 km from the other 2. Grids were >300 m from a road, and each grid was 4 ha in size. Forty-one pitfalls were placed at 25-m intervals on each grid. We constructed pitfalls of 2 number 10 cans as described by Corn (1994); small holes were punched in the bottom of each can to allow water to drain. A raised wooden lid covered each pitfall; we used no drift fences. Pitfalls were run as live-traps and were checked at least every 2 d from late May to early September, 1989–1991, for a total of about 5100 trap-days per grid per year (Table 1). Each capture was identified, the sex and age determined, and 1 toe clipped to identify recaptures.

We measured habitat characteristics at each trap location on each grid. A 5-m-radius plot was centered on each trap location and the number of live trees counted by height class (<1.5, 1.5–3, >3–6, and >6 m). A line transect was randomly placed across each plot, and the type of ground (e.g., rocks, litter), shrub (<1.5 m tall), and canopy (by height class 1.5–3, >3 m) cover was visually determined at 1-m intervals along the transect.

Spearman's correlation was used to compare rank abundance of species (i.e., similarity) between grids. Habitat characteristics were compared among species, and between species and grid habitat abundance, using analysis of variance followed by Tukey's multiple comparison tests. Relationships among species abundance on each grid were examined using product-moment correlation. Multiple regression analysis with stepwise inclusion of variables was used to relate animal abundance and habitat characteristics. Variables were entered at $P < 0.1$.

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TABLE 1. Index of abundance for reptiles on 3 trapping grids, Inyo Mountains and White Mountains, California, 1989–1991. Values are number of animals per 1000 trap-days.

	Grid			
Species	Pinyon	Cedar	Westgard	Overall
Trap-days	15,900	15,500	14,700	46,100
Cnemidophorus tigris	0.00	0.00	3.61	1.15
Eumeces gilberti	0.31	0.71	0.75	0.59
E. skiltonianus	0.69	0.97	0.20	0.63
Sceloporus graciosus	12.26	10.90	19.25	14.03
S. occidentalis	12.33	6.00	7.48	8.66
Uta stansburiana	3.02	0.84	3.47	2.43
TOTAL	28.61	19.42	34.76	27.49

Six lizard species were captured during the study, although *Cnemidophorus tigris* was captured only on the Westgard grid (Table 1). *Sceloporus graciosus* (51% of total captures) and *S. occidentalis* (32%) were the most abundant species, and at least 1 individual of each species was captured at 93% and 88%, respectively, of traps (see sample sizes in Table 2). *Uta stansburiana* totaled only about 9% of all captures, but occurred at 41% of all traps. The 2 *Eumeces* species were relatively scarce, occurring in only 16–18% of traps. Rank abundance of species was significantly correlated between Pinyon and Cedar grids ($r = 0.89$, $P = 0.03$) and was positively but not significantly correlated between Pinyon and Westgard ($r = 0.54$, $P = 0.30$) and Cedar and Westgard ($r = 0.49$, $P = 0.36$).

The only consistent patterns across all grids were weak ($r = 0.23–0.33$, P's $= 0.05–0.15$) positive correlations between abundance of *Cnemidophorus tigris* and *Eumeces gilberti*. On Westgard, *C. tigris* was also significantly correlated with *Uta stansburiana* ($r = 0.4$, $P < 0.01$) and had a tendency to be correlated with *Sceloporus graciosus* ($r = 0.3$, $P < 0.1$). *E. gilberti* on Westgard was correlated with *E. skiltonianus* ($r = 0.62$, $P < 0.001$) and *U. stansburiana* ($r = 0.33$, $P < 0.05$). The only other significant relationship was between *S. graciosus* and *E. gilberti* on Cedar ($r = 0.38$, $P < 0.05$). No negative abundance relationships were found.

Habitat characteristics showed few differences among species (Table 2). *Cnemidophorus tigris* occupied traps that were near slope bottoms and had more bare ground, fewer pinyon trees, and more juniper trees, relative to all other species. *Uta stansburiana* also tended to occupy traps with greater bare ground, fewer pinyon trees, and more juniper trees ($P < 0.1$). Down wood had little association with reptile occurrence. Multiple regression analyses accounted for $>10\%$ of variation between animal abundance and habitat characteristics only in *Cnemidophorus tigris*, where species abundance increased with increasing cover of bare ground ($r = 0.54$) and stones ($r = 0.16$; adjusted $R^2 = 27\%$). Simple correlation between animal abundance and habitat characteristics found increases in abundance of *Eumeces gilberti* ($r = 0.23$) and *Uta stansburiana* ($r = 0.31$) with increasing bare ground (P's < 0.01). Positive association between slope position and abundance was also shown for *E. gilberti* ($r = 0.20$), *E. skiltonianus* ($r = 0.23$), and *Sceloporus occidentalis* ($r = 0.17$; P's < 0.05). Lastly, a positive relationship was found between cover of pinyon trees and *S. occidentalis* ($r = 0.28$, $P < 0.001$).

We found the herpetofauna of the pinyon-juniper woodland to be predominated by widespread occurrence and relatively high abundance of *Sceloporus graciosus* and *S. occidentalis*, widespread occurrence but low abundance of *Uta stansburiana*, and relatively sparse occurrence and abundance of 4 additional species. *Sceloporus* appeared to separate slightly based on tree density, with *S. occidentalis* found at higher abundance in denser patches of pinyon trees. Marcellini and Mackey (1970) found that *S. graciosus* preferred more shrubby and open areas relative to *S. occidentalis*, and that *S. occidentalis* was partially arboreal. Adolph (1990) showed that these 2 *Sceloporus* used similar microhabitats in sympatry because they responded similarly to thermal conditions. Lastly, Rose (1976) concluded that the 2 species segregated in sympatry based on differences in microhabitat use and were able to coexist despite extensive overlap in prey use. Thus, our findings of only slight habitat separation, with *S. occidentalis* using areas with relatively more trees, are consistent with previous work. The lack of negative correlation between abundance of any species indicates that no overt interspecific interference is evident in the pinyon-juniper community.

Cnemidophorus tigris showed the highest degree of habitat specificity; it occurred only

TABLE 2. Habitat characteristics for reptiles captured in pitfall traps, Inyo Mountains and White Mountains, California, nal was captured); numbers presented are means (*s*), rounded for ease of presentation.

	Cnemidophorus tigiris ($n = 18$)	*Eumeces gilberti* ($n = 20$)	*Eumeces skiltonianus* ($n = 23$)
Slope position (0–1)	0.18 (0.29)A	0.61 (0.33)B	0.67 (0.29)B
Percent cover			
Bare ground	30 (28)A	14 (17)AB	13 (17)B
Stone	55 (29)	52 (20)	44 (16)
Shrub	8 (7)	10 (10)	9 (10)
Down wood	3 (5)	3 (5)	5 (6)
Pinyon trees	12 (24)A	39 (32)B	39 (31)B
Juniper trees	14 (18)	2 (5)	3 (8)

[a] P associated with analysis of variance (ANOVA).

[b] For significant ANOVA ($P < 0.05$), means within rows with unlike capital letters (e.g., A, B) were significantly different by Tukey's multiple comparison test.

on the grid (Westgard) with most open ground, lowest density of pinyon trees, and highest density of juniper trees. *Uta stansburiana* and *Eumeces gilberti* showed similar, although weaker, relationships with habitat variables we measured; both species attained highest abundance on Westgard. Our results complement those found in other studies where these species were shown to occupy relatively warmer, open sites (e.g., Banta 1962, Pianka 1970). Habitat used by the 2 skink species was similar, except that *E. gilberti* occupied more open sites. Previous research has indicated that *E. gilberti* occurred in warmer, lower-elevation sites than *E. skiltonianus* (Rodgers and Fitch 1947, Tanner 1957). Our results indicate that, within an area of sympatry, these skinks overlap broadly but show slight microhabitat separation based on openness of vegetation.

Our results indicate that the predominant feature of the pinyon-juniper environment separating species is a gradient reflecting subtle differences in pinyon and juniper tree cover. Within the pinyon-juniper woodland, differences in shrub, litter, and rock cover had no obvious influence on animal abundance. A possible exception was the desert night lizard (*Xantusia vigilis*), a species we visually observed adjacent to the Pinyon grid under thin rock slabs (but did not capture in pitfalls; see Morrison and Hall in press).

Natural or human-induced changes in tree density appear to be the factor most likely to cause substantial changes in the lizard community. For example, the use of pinyon and to a lesser extent juniper as fuelwood could be regulated to avoid substantially changing tree density. Although not practiced in our study region, large-scale removal of pinyon and juniper trees to promote grasslands (e.g., via chaining) for use by livestock and big game could have a detrimental impact on herpetofauna. Incorporation of herpetofauna into management plans could help alleviate negative impacts on the distribution and abundance of species on a local and regional scale.

We thank personnel of the White Mountain Research Station (University of California), especially E. Phillips and D. Trydahl, for logistical support. Some of this project was performed while the authors were affiliated with the Department of Environmental Science, Policy, and Management, University of California, Berkeley. We thank our field assistants, P. Aigner, L. Baker, J. Block, L. Ellison, A. Mellow, L. Nordstrom, and S. Shoemaker.

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1989–1991. Data are for traps in which the species was captured at least once (n = number of traps where at least 1 individ-

Sceloporus graciosus (n = 114)	*Sceloporus occidentalis* (n = 108)	*Uta stansburiana* (n = 50)	Overall site (n = 123)	$p^{a,b}$
0.49 (0.36)B	0.51 (0.35)B	0.47 (0.37)B	0.50 (0.35)B	0.001
12 (16)B	12 (16)B	17 (22)AB	11 (16)B	0.001
50 (21)	48 (21)	51 (23)	50 (21)	0.650
8 (9)	7 (8)	8 (9)	7 (9)	0.742
3 (5)	3 (5)	3 (5)	3 (5)	0.754
43 (45)B	46 (46)B	33 (35)B	43 (45)B	0.054
7 (13)	7 (13)	9 (16)	7 (13)	0.084

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DISTRIBUTION OF *PINUS MONOPHYLLA* IN THE NORTHERN WASATCH RANGE OF UTAH

Robert Weiss[1]

Key words: singleleaf pinyon, Pinus monophylla, *Wasatch Mountains, Utah, range extension.*

Pinus monophylla (singleleaf pinyon) is a coniferous tree species that forms extensive woodlands with *Juniperus osteosperma* (Utah juniper) in the Great Basin region. Its distribution includes Nevada, parts of eastern California, western Arizona, southern Idaho, and western Utah (Fig. 1). Averaging 4.5–9 m tall and reaching heights of over 12 m, it grows on pediments, slopes, and ridges, while rarely being found on valley floors. *Pinus monophylla* woodlands are relatively short in stature and usually form a band above sagebrush shrublands and below lower montane forests. *Pinus monophylla* grows under more xeric conditions than any other pine in the United States (Meeuwig et al. 1990). It is replaced by *P. edulis* (Colorado pinyon; Fig. 1) in the eastern part of its range, where summer precipitation exceeds about 8 cm (Tueller et al. 1979). *Pinus monophylla* is limited in the northern part of Nevada and Utah and southern Idaho by temperature minima and duration of low-temperature events (West et al. 1975).

Disjunct populations of *P. monophylla* in the northern Wasatch Mountains of Utah are 110 km from the nearest station of *P. monophylla*, which are in the Black Pine Mountains of southern Idaho (Lanner and Hutchison 1972). These stands in northeastern Utah were proposed by Lanner and Hutchison (1972) to be remnants of a climate with environmental conditions more favorable for *P. monophylla* establishment and are probably persisting "between survival and extinction." This note describes newly found populations of *P. monophylla*, discovered in 1995–96, representing a northern extension of this species in the Wasatch Range in Utah (Fig. 1). Vouchers are at the herbarium at Utah State University (USU).

The area studied is in the Wasatch National Forest, Logan Ranger District. Both sites are in lower Logan Canyon, characterized by steep slopes, cliffs, and rocky terrain (Fig. 1). One site is Card Canyon, 14.5 km east of Logan and Utah State University. The other is Right Fork Logan Canyon, approximately 3 km northeast of Card Canyon. These sites are approximately 8–11 km northeast of those described by Lanner and Hutchison (1972). *Pinus monophylla* stands at Card Canyon are found at elevations of 1770–1920 m, those at Right Fork Logan Canyon at 1830–1980 m.

The stands occur on southerly aspects where overstory vegetation is composed primarily of juniper woodland with *P. flexilis* (limber pine) and *Pseudotsuga menziesii* (Douglas-fir) at higher elevations. *Juniperus osteosperma* is the dominant conifer at the Card Canyon site, and *J. scopulorum* (Rocky Mountain juniper) at Right Fork Logan Canyon. The north aspect of Right Fork Logan Canyon, at 2010 m elevation, has a stand of more than 20 *Abies concolor* (white fir), also a rare species in this part of the northern Wasatch of Utah. Soils are stony colluvium, while parent materials are mainly calcareous or quartziferous. Annual precipitation averages 46.5 cm at USU (elevation 1457 m) to 101.9 cm at the school forest (elevation 2591 m). Snowfall averages 188 cm at USU annually.

After initial discovery of the new stands of *P. monophylla* in the northern Wasatch east of Logan, I conducted several surveys to locate more trees. Most individual pinyons are located on very steep, rocky terrain, which makes travel arduous. On several dates between 1995 and 1997 I conducted a walk-through to locate more pinyons. With this method, the entire

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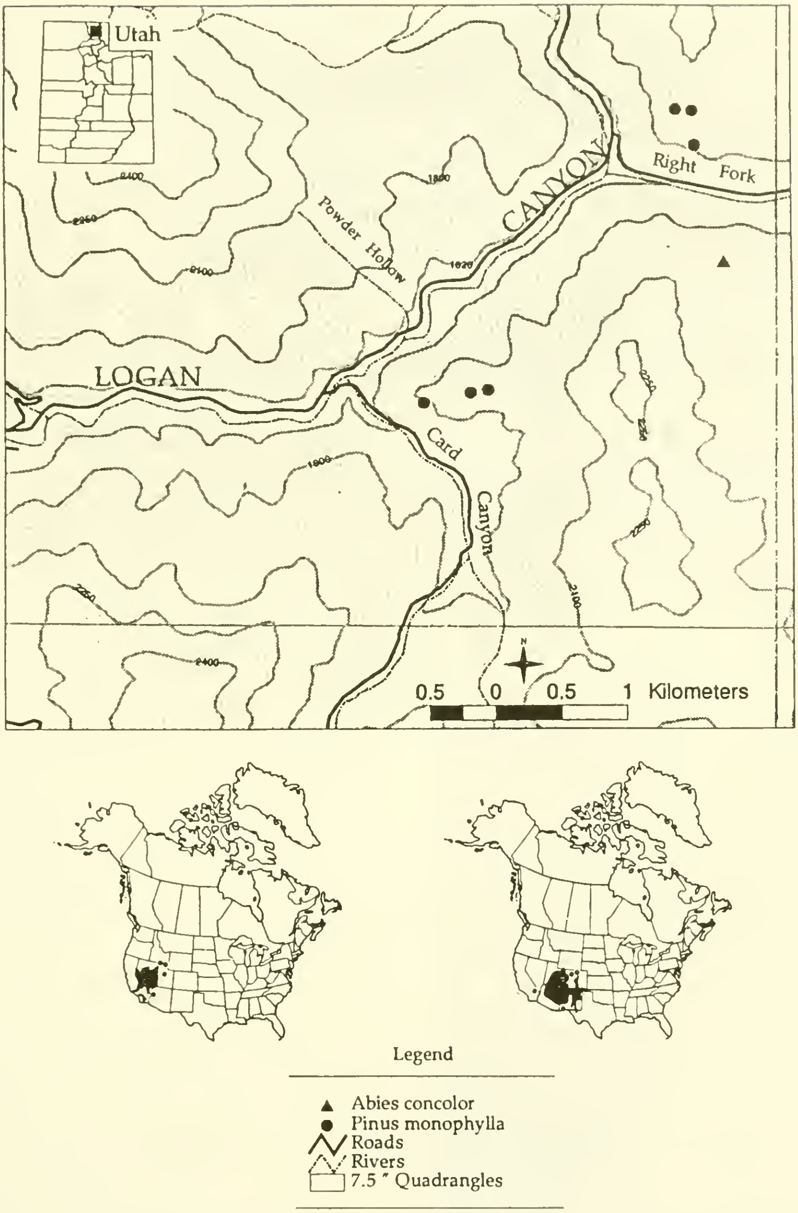
Utah
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Powder Hollow
LOGAN
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2250
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1920
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N
Legend
▲ Abies concolor
● Pinus monophylla
Roads
Rivers
7.5 ″ Quadrangles

Fig. 1. Upper map is of *Pinus monophylla* and *Abies concolor* stand locations in the northern Wasatch Range, 15 km east of Logan, Utah. Distribution maps are of *Pinus monophylla* (lower left) and *Pinus edulis* (lower right). Distribution maps taken from Flora of North America Editorial Committee (1993).

area surrounding the *P. monophylla* was visually inspected.

Seven *P. monophylla* were recorded at the Card Canyon site and 5 at the Right Fork Canyon site. Pinyons at Card Canyon are 8 km northeast of those described by Lanner and Hutchison (1972) in Lower Logan Canyon. Several individuals <2 m tall indicate these stands are regenerating. Every visit and inspection of the stands revealed pinyon trees with only 1-needled fascicles (*P. edulis* has fascicles of 2 needles), suggesting no hybridization with *P. edulis*.

Aspects range from southeast to west, with no individuals on northerly aspects. The individuals vary in size from seedlings to specimens over 12 m tall. Several of the trees are located on rock outcrops, indicating very little soil and minimal competition from other plant species. Fuel loads are light in these locations, possibly giving them added protection from wildfires. Four of the individuals are producing cones.

Additional research could analyze *P. monophylla* for hybrids at the Card Canyon and Right Fork sites in the future. Lanner and Hutchison (1972) found some *P. monophylla* and *P. edulis* hybrids in some of their pinyon locations in the northern Wasatch, but their pinyon site in lower Logan Canyon is pure *P. monophylla.*

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DISTRIBUTION OF THE SPECIES *PHRYNOSOMA PLATYRHINOS* IN UTAH

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Key words: Phrynosoma, *Utah, species distribution.*

A study of the genus *Phrynosoma* by Reeve (1952) places *Phrynosoma platyrhinos platyrhinos* in the Uinta Basin in northeastern Utah. His accompanying range map (Reeve 1952: fig. 3) extends the range of this species from the Great Basin of Utah east across the central highlands into the upper Colorado River Basin of northeastern Utah. *Phrynosoma platyrhinos* is a desert species ranging primarily in the Great Basin and does not occur in the mountains and high plateaus of central Utah. Reeve lists 5 specimens from the upper Colorado River Basin. These specimens are in the Brigham Young University (BYU) herpetological collection: 2 are from Uintah County (25 mi SE of Jensen [BYU 2637] and 3 mi E of Ouray [BYU 345]), and 3 are from Carbon County (Price [BYU 1029, 1030, 8033]).

The 2 from Uintah County and a 3rd specimen (BYU 647) are *P. platyrhinos* but are best placed in the subspecies *P. p. calidiarum.* Figure 1 indicates my present concept of the distribution of *P. platyrhinos* in Utah, based on examination of the now available specimens in the BYU herpetological collection. I have examined the 3 specimens listed by Reeve (1952) for Carbon County (BYU 8033, 1029, 1030, collected by S. Flowers). They are typical examples of *Phrynosoma hernandesi* (Zamudio et al. 1997). Six BYU specimens from Carbon County (at or near Price) are also *P. hernandesi,* as are 18 specimens from eastern Emery County. This suggests that *P. platyrhinos* has not succeeded in crossing the high plateaus north of the Wahweep depression (north from Crossing of the Fathers) nor the Colorado River in eastern Kane County. Apparently, Reeve assumed, based on his distribution map, that those *Phrynosoma* occurring in the eastern foothills of the central highlands would be *P. platyrhinos.*

Pianka (1991: map 517.1) provides a near duplication of the range map of Reeve (1952), and thus includes the incorrect distribution and misidentified specimens listed by Reeve for Carbon County, Utah.

Those previously mentioned specimens collected near Jensen were taken at Willow Creek, SE of Ouray (BYU 345), and at Deadman's

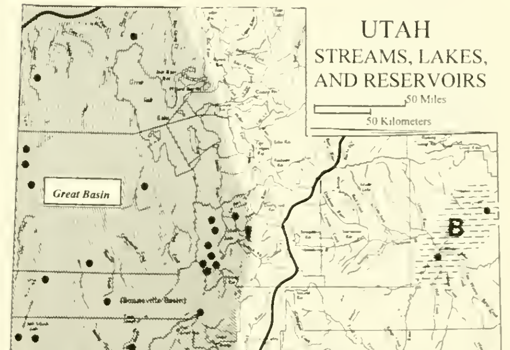

Fig 1. Distribution of *Phrynosoma platyrhinos* in Utah, based on specimens in the BYU herpetological collection: A. *P. p. platyrhinos;* B. *P. p. calidiarum.* Map taken from Greer et al. (1981).

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Flat, 25 mi SE of Jensen (BYU 2637). Since the Yampa and White rivers enter the Green River not far from the areas where the specimens were collected, I asked Rosanne Humphrey and Hobart Smith, both at the University of Colorado, for any *P. platyrhinos* locality records for western Colorado. They replied that no records are presently available in the University of Colorado Museum. Thus, the occurrence of *P. p. calidiarum* in Uintah County, with no locality records for Grand County and none for San Juan County north of the San Juan River, leaves the population in Uintah County as an isolated and disjunct population. Stebbins (1985: map 98) extends *P. p. calidiarum* into southern San Juan County, but gives no indication of its presence north of the San Juan River. Hardy (1938) lists only *P. hernandesi* for Carbon County, Utah.

A series of *Phrynosoma p. calidiarum* extending in southwestern Utah east from Kanab, Kane County, to the Colorado River provides a continuous range extension into the deserts of southern Utah. These locality records (BYU 14975, 7 mi E of Kanab; BYU 11216–11220, 11383, 14196, approx 39 mi E of Kanab; BYU 12906, Adairville; BYU 11299–11300, East Clark Bench, 8 mi E of Adairville; and BYU 14888–14893, 16663–16665, 18922, Crossing of the Fathers) indicate a substantial population in the valleys between the Vermilion Cliffs and the Grand Canyon Plateau. However, there are no locality records for *P. platyrhinos* east of the Colorado River in either San Juan or Grand counties.

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FIELD OBSERVATIONS ON THE MYRMECOPHILOUS BEETLE *ARAEOSCHIZUS AIRMETI* TANNER (COLEOPTERA: TENEBRIONIDAE) AT HARVESTER ANT (HYMENOPTERA: FORMICIDAE) MOUNDS

Paul Hendricks[1] and Lisa M. Hendricks[1]

Key words: Araeoschizus airmeti, *myrmecophily,* Pogonomyrmex salinus, *symbiosis, Idaho, beetles, ants.*

Beetles in the tenebrionid genus *Araeoschizus* frequently are found with colonies of several ant species (Tanner 1945, Lavigne 1969, Papp 1981, Wheeler and Wheeler 1986, Clark et al. 1986). On occasion, however, *Araeoschizus* has been captured in pitfall traps (Papp 1981, Stafford et al. 1986), indicating that these beetles are sometimes active on the ground surface apparently away from ant colonies. Because of this observation, some biologists question whether *Araeoschizus* spp. are true myrmecophiles (see Papp 1981); additionally, the genus is not listed by Hölldobler and Wilson (1990) in their table of invertebrates symbiotic with ants.

Little information is available on behavior and ecology of *Araeoschizus* in the presence of their ant hosts, and the frequency of ant colonies occupied by these beetles has not been reported previously. In colonies of the harvester ant *Pogonomyrmex occidentalis* (Cresson) at a site in Wyoming, Lavigne (1969) found as many as 188 *A. armatus* Horn in seed and trash chambers to depths of about 160 cm. Beetles tended to be gregarious, with as many as 64 occupying a single chamber. Beetles were first found near the ground surface in the mound proper in April. Lavigne (1969) noted that at a 2nd site, *Araeoschizus* was not found associated with ants. In Idaho, *A. airmeti* Tanner was collected in June from seed chambers 9–10 cm below ground surface in a colony of *P. salinus* Olsen (Clark and Blom 1988). In Idaho and Oregon, Hendricks (1991) collected several individuals (>1 per colony) of *A. airmeti* in March at 3 widely separated colonies. Beetles were found in the presence of ants on undersides of stones partly buried in mound tops of *P. salinus.*

On 13 April 1998 we walked a 1.6-km transect near Black Butte, Elmore County, Idaho (43°03′30″N, 116°11′30″W; 854 m elevation), crossing an area sparsely covered with vegetation (including *Artemisia* and *Chrysothamnus*) growing on sandy soils overlying basalt flows. While walking the transect (09:35–10:50 MDT), we paused for brief periods (not more than 5 min each) at harvester ant (*P. salinus*) mounds where workers were active on the surface, and documented the presence or absence of *A. airmeti.* Weather was overcast, windy, and cold (7.5°C). As a consequence, <10 worker ants were present on the surface of any mound, and most ant activity was confined to a distance <10 cm around any entrance. Workers were sluggish and slowly removing germinating seed, dead workers, and detritus from the colonies. The small midden size around mounds indicated that cleaning of colonies had been underway for only a relatively short time.

We observed 19 *A. airmeti* around entrances at 11 (73.3%) of 15 mounds examined. Single beetles were noted at 6 mounds, 2 beetles at 4 mounds, and 5 beetles at 1 mound. Fourteen (73.7%) of the beetles at 9 mounds were carried in the mandibles of worker ants, some as they emerged from entrances at the time we first detected them. The number of beetles transported by ants was significantly different from that predicted (goodness-of-fit test, Williams's correction: $G = 4.318$, $df = 1$, $P < 0.05$), assuming equal probability of being carried or not. Most beetles were grasped around the elytra and carried lengthwise, with the anterior end pointed forward. Beetles were transported 3 and 8 cm from mound entrances in the 2 cases measured, then released by the ants. Beetles carried by ants resisted transport by grasping pebbles or twigs with their tarsi, rather than by vigorously struggling. In one case an ant persisted in carrying a beetle for 5 min before releasing it. In 2 cases resistance by beetles apparently agitated the transporting ants, which brought their abdomens forward ventrally, and they attempted to sting (we did not detect an extended stinger) or spray the beetles. Nevertheless, transporting ants did not injure any of the beetles. Released beetles tended to wander around on the mound, but in 6 instances the beetles immediately returned to the entrance and reentered the mound, passing other ants without additional interference.

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The frequency with which we found *A. airmeti* around harvester ant colony entrances and the passive response often shown by ants to their presence indicate that this beetle is adapted for living with ants, as suggested previously by other authors (e.g., Papp 1981, Clark and Blom 1988). Clark and Blom's (1988) description of behavior between captive ants and beetles closely matches what we observed in the field; i.e., beetles are transported some distance by ants and then released. Clark and Blom (1988) noted that ants sometimes appeared to sting beetles if they struggled, as we also observed, but we observed no beetle injuries by ants. Ants appeared to ignore beetles returning to colony entrances.

Presence of *A. airmeti* on the surface of ant mounds when seed chambers were being cleaned by worker ants in a large percentage of our sample, and the large percentage of beetles carried by the ants, suggest that many beetles were occupying seed chambers at the time of our observations. *Araeoschizus* has been found in seed chambers of harvester ants throughout the year (Lavigne 1969, Clark and Blom 1988), although it is not known if ants carry beetles to the surface of mounds as long as the ants are active there. Nor is it known why harvester ants remove beetles from seed chambers. Possibly, ants mistake beetles for germinated seeds or detritus, or perhaps beetles release a chemical that promotes their transport by the ants, as has been conjectured for myrmecophilous pselaphid beetles (e.g., Leschen 1991). It could be advantageous for beetles to be moved to the ground surface, as was suggested by Hendricks (1991), analogous to the advantages of hilltopping (see Shields 1967, Alcock 1987). Concentration of beetles in a reduced space during a short span of time could increase opportunities for encountering potential mates, although nothing is presently known regarding sex ratios of beetles found throughout ant colonies, let alone near the surface. *Araeoschizus* may also make dispersal movements between colonies, judging by the presence of beetles in pitfall trap samples (Papp 1981, Stafford et al. 1986). One benefit of intercolony dispersal would be the reduction of inbreeding, but, again, nothing is yet known about the frequency or cause of surface activity and movements away from ant colonies.

We thank Bill Clark and Paul Blom for drawing our attention to their papers several years ago, and Bill Clark for comments on an earlier version of the manuscript. Determinations of earlier collections from the study site were provided by John Doyen (University of California, Berkeley) and Frank Merickel (University of Idaho) for beetles and ants, respectively. Vouchers are deposited with the University of California, Berkeley (beetles) and the authors' private collection (beetles and ants). Kit and Carson waited patiently while we inspected ant mounds, when they would have preferred to hunt rabbits.

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BOOK REVIEW

A Guide to the Trees of Utah and the Intermountain West. Michael Kuhns. Utah State University Press, Logan, Utah 84322-7800. 1998. $14.95, softcover.

This compact 4.5 × 8.5-inch book of 341 pages provides names, descriptive characteristics, and relevant line drawings for 219 woody species. All trees native to Utah and most introduced trees and treelike shrubs that can be grown successfully in the state are included. Although the book does not list all species that potentially could be grown in the warmer southern regions of Utah, it does suggest additional references should this information be desired.

Whereas the main body of the work is devoted to names, descriptions, and drawings, introductory information provides the nonprofessional reader with a workable vocabulary for basic understanding. Each species is consistently evaluated according to morphology of leaves, twigs/buds, flowers/fruit, bark, and wood. Much of this comparative information is superfluous, but it has made the treatment consistent. Less information is provided for less common species. General information concerning place of origin, ecological requirements, and light requirements is normally provided for each species as well as landscape use and plant hardiness zone recommendations. All native species are clearly marked with a symbol so they stand apart.

The author chose to arrange species within the text by the traditional similarity approach rather than alphabetically according to family. This generally means that one is obliged to look up the tree in the index by species name or by common name and then find it by page number. I personally find the nonalphabetical arrangement awkward because it requires looking up information twice.

Most species listed are accompanied by superb black-and-white line drawings that have been borrowed by permission from other publications. They greatly enrich the text since written descriptions of cones, flowers, and fruits do not convey comparative information as quickly or as well. The 12 color photos presented near the middle of the book seem out of place and merely whet the appetite for more.

A key to 172 of the 219 species is provided so that one may work through a series of couplets and independently discover the identity of an unknown tree. The key is easy to use, but as with all keys, experience and intuition help. Leaving 47 species out of the key is a serious flaw. Nearly 1/3 of the trees I attempted to key were not included. Anyone depending on the key to identify a tree would probably find this experience confusing. The key has the same weakness as most keys in that it is written to assist the amateur, but its operation requires more knowledge than the average person possesses. For example, a novice trying to key *Sophora japonica*, using this key, would be baffled by insistence that its fruit is a legume (described in the glossary as a pod that splits). This particular tree has a loment, an unusual kind of legume that does not resemble a pod that splits. Either the key or the glossary should explain this unusual fruit; both fail in this case. Keys give amateurs independence, but in order to be totally useful, they need to be complete. Both the key and the glossary should be written with the layman foremost in mind.

Notwithstanding embarrassing mistakes, such as a color photograph of an atlas cedar inadvertently labeled as a bristlecone pine, this book will be a useful resource for those wishing to learn about the woody species growing in the Intermountain region. It will also be helpful to homeowners and professionals interested in selecting plants for landscaping purposes. It summarizes much practical information on species requirements, growth patterns, ultimate size, zone hardiness, site selection, planting, climatic considerations, and common cultivars. I find this book a valuable addition to my library and plan to use it in my field botany class. I recommend its use to those interested in learning about the woody vegetation of Utah.

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CHROMOSOME RACES IN *SARCOBATUS* (SARCOBATACEAE, CARYOPHYLLALES)

Stewart C. Sanderson[1], Howard C. Stutz[2], Mildred Stutz[2], and Richard C. Roos[3]

ABSTRACT.—*Sarcobatus* Nees., a genus of North American halophytic shrubs, consists of 2 species: *S. vermiculatus* (Hook.) Torr. ($n = 18, 36$), which is widespread in western North America, and *S. baileyi* Cov. ($n = 54$), endemic to Nevada. Within *S. vermiculatus*, populations of $n = 36$ are widely distributed, whereas populations of $n = 18$ are found only in the Sonoran Desert, northern California, and northwestern Great Plains, locations at the periphery of the species range. Although the chromosome number of $n = 18$ is apparently tetraploid, failure to form an $n = 27$ race intermediate to those of $n = 18$ and $n = 36$ suggests that $n = 18$ *S. vermiculatus* is of significant age and that it behaves chromosomally as a diploid. *Sarcobatus* has a long fossil pollen record and endured Pleistocene climatic extremes with little range displacement.

Key words: Sarcobatus, *polyploidy, autoploidy, diploidization, Pleistocene distributions.*

Sarcobatus Nees. is an endemic North American genus consisting of spiny shrubs that are monoecious and wind-pollinated, with reduced, fleshy leaves. It has historically been placed in the Chenopodiaceae (order Caryophyllales). Like members of subfamily Salsoloideae (Spirolobeae) in the Chenopodiaceae, the embryo of *Sarcobatus* is elongate and coiled in seed, enabling rapid extension during germination. In common with the chenopod genera *Spinacia*, *Atriplex*, and *Ceratoides*, plants of *Sarcobatus* contain 6-oxygenated flavonoids (Sanderson et al. 1988). Of 12-plus families in the Caryophyllales, 6-oxygenated flavonoids are otherwise known to date only from the Amaranthaceae and Aizoaceae (Rodman 1994). *Sarcobatus* propagules, formed from the winged calyx of female flowers, are adapted for wind dispersal across barren surfaces such as mud flats or sand dunes (Danin 1996). The segments of this calyx are accrescent and enclose the seed in fruit (Standley 1916, Welsh et al. 1993), somewhat like that of some chenopods.

In spite of these similarities to the Chenopodiaceae, other *Sarcobatus* characteristics are discordant within that family. Macromolecular and sieve-tube plastid evidence suggests a linkage of the genus to other families, particularly the Nyctaginaceae and Phytolaccaceae (Behnke 1993, 1994, Downie et al. 1997).

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A feature of *Sarcobatus* not duplicated in any related family is the male inflorescence in which numerous, asepalous flowers are borne in a conelike structure formed from peltate scales. In view of the distinctiveness of *Sarcobatus*, a separate family, Sarcobataceae, has recently been created for it (Behnke 1997).

Fossil pollen of *Sarcobatus* has been found in Eocene, Oligocene, and later strata from localities in Washington, Oregon, Idaho, Wyoming, and Colorado (Leopold and Macginitie 1972, Leopold and Denton 1987); the genus was present in late Miocene in the area of Jackson Hole, Wyoming, before the present Teton Mountains were uplifted (Barnosky 1984). Because floras during the early and mid-Tertiary were considerably more tropical and preponderantly arboreal (Leopold and Macginitie 1972), *Sarcobatus* may have had somewhat different environmental tolerances at that time than it does at present. However, it would likely have grown on the margins of dessicating lakes rather than within forests.

Sarcobatus at present consists of 2 species, *S. vermiculatus* (Hook.) Torr., of wide distribution in western North America, and *S. baileyi* Cov., which is limited to the central and western parts of Nevada in the Great Basin. *Sarcobatus vermiculatus* occupies saline bottomlands, playa dunes, and badlands, while *S. baileyi* is found on arid slopes, usually in monotypic stands or in association with *Atriplex confertifolia*.

The only published chromosome count for *Sarcobatus* of which we are aware is $n = 18$, from a collection of *S. vermiculatus* near Medicine Hat, Alberta (Bassett and Crompton 1970). The Chenopodiaceae and Phytolaccaceae have base chromosome numbers of $x = 9$ (Turner 1994). Although the Nyctaginaceae has a variety of chromosome numbers, Turner (1994) suggests its base may be $x = 10$. Nevertheless, $x = 9$ would be a plausible alternative. *Sarcobatus* is somewhat isolated phylogenetically, but it seems likely, in view of its relationships with these families, that $x = 9$ is its base number as well.

It is our purpose to report on the distribution and morphological characteristics of the chromosomal races we have encountered within taxa of the new family Sarcobataceae, and to present available evidence regarding their origin and genetics.

MATERIALS AND METHODS

Chromosome counts, leaf-flavonoid content, and morphological measurements of *Sarcobatus* were obtained from sites throughout its range, and representative voucher specimens have been deposited at BRY. Cytological and chemical methods have evolved somewhat during accumulation of data for this report (1982–1996). The following procedures are currently used.

Chromosome Counts

We have found the use of 5% acetic acid or an equivalent strength of household vinegar to be safer for field use and to give results comparable to those of alcohol-acetic acid in fixation of meiotic material for taxa of the Chenopodiaceae and *Sarcobatus* (Stutz and Sanderson 1983, Sanderson and Stutz 1994). We determined chromosome counts from pollen mother cells of male flower buds fixed in vinegar (5% acetic acid strength) and refrigerated (2°C) or frozen (–20°C) for up to several months before examination. Anthers were squashed in acetocarmine stain, which was concentrated to supersaturation by means of evaporation on the microscope slide. Preparations were preserved by replacement of the dye solution under the cover slip with 45% acetic acid, and then with corn syrup, thinned as necessary with vinegar, which retarded mold growth in the syrup solution better than did 5% acetic acid. A few additional counts were made from root tips using methods described by Stutz and Sanderson (1983).

Flavonoids

Determination of aglycone moieties of foliar flavonoids was carried out upon either 25 cc of crushed air-dried leaves or a similar volume of 5% acetic acid–preserved leaf material. Samples were hydrolyzed for 60 min in 1N HCl over a boiling water bath to remove glycosidic sugars, then ground in 85% aqueous methanol, filtered, and washed with additional 85% methanol. The combined filtrate and washings (50 mL total) were mixed with an equal amount of water and then extracted with 50 mL of ethyl acetate, and again afterwards with a small rinse. The combined ethyl acetate extract and rinse was blown down with compressed air and the residue extracted with 1–2 mL 45% acetic acid, which was then applied to half-sheets of Whatman 3M chromatography paper. Chromatography was carried out as reported previously (Sanderson and Stutz 1994), and sheets were thoroughly air- or oven-dried between 1st- and 2nd-dimensional chromatography. Most flavonoid compounds occurring in *Sarcobatus* have been previously isolated and chemically identified (Sanderson et al. 1988).

Morphology

Morphological characteristics of mature *Sarcobatus* plants in natural populations were measured in late summer 1995. Measurements were pooled from 5 plants in each population and compared statistically by taxon, ploidy, and geographic area using ANOVA (Proc GLM) and the Studentized Maximum Modulus (GT2) means comparison test for unequal sample sizes (SAS Institute 1989). Characteristics measured were plant height and width, leaf length and width (measured from a large leaf on the branch nearest the investigator), and male inflorescence length (excluding peduncle). Male inflorescence width could not be included because inflorescences in *S. baileyi* had already shed most of their scales at the season in which measurements were taken.

RESULTS

Original chromosome counts representing 224 localities (Fig. 1, Appendix) were obtained in this study. *Sarcobatus* chromosomes are small, but large enough for figure-8 bivalents to occur at a moderate frequency (Fig. 2). Meiosis appeared to be regular in both diploid ($n = 18$) and octoploid ($n = 36$) *S. vermiculatus* plants as well as in 12-ploid ($n = 54$) *S. baileyi*. Abnormalities such as multivalents were observed only rarely, and spontaneous increase to higher ploidy appears to be relatively rare.

Except where there was geographic overlap of races of different ploidy levels, populations containing individuals of a higher ploidy occurred in only a few cases (Appendix). In 2 of 166 apparently octoploid populations of *S. vermiculatus* that were sampled, a single 12-ploid individual was also encountered. One population was located northwest of Tonopah, Nevada, and the other near Willard, New Mexico. Individuals of intermediate chromosome numbers of approximately 9-ploid to 10-ploid, apparently representing backcrosses of 12-ploid individuals to parental octoploid plants, were encountered in 6 additional instances. However, no plants of higher chromosome numbers were identified within populations of tetraploid *S. vermiculatus*, nor in *S. baileyi*.

Octoploid populations of *S. vermiculatus* were found to occupy the majority of the species range, from Montana and the Dakotas to northern Arizona, and from Colorado and Nebraska westward to California (Fig. 1). Tetraploids were limited in the north to Alberta, Saskatchewan, northern Montana, and North Dakota; in the west they occurred in Mono and Modoc counties of eastern California.

In a somewhat different ecological setting at the southernmost part of the species range, extensive populations of *S. vermiculatus* have been reported in the Gran Desierto of northern Sonora (Ezcurra et al. 1988), growing in coastal areas with shallow water tables, upon partially stabilized sand dunes and at the edge of salt pans. Our samples showed that these plants are tetraploid. A few small populations of similar tetraploid plants are found near the Gila River in southern Arizona, growing on sandy sites in areas unmodified by agriculture. Except for the Sonoran Desert plants and a few rare octoploids at northern extremes or higher elevations, *Sarcobatus* is otherwise absent from the Chihuahuan, Sonoran, and Mojave warm deserts of the southwestern United States and Mexico.

Tetraploid and octoploid populations growing in close proximity were encountered in the upper Pit River drainage, at Goose Lake on the California-Oregon border, and at sites in Montana and North Dakota (Fig. 1, Appendix).

In a mixed-ploidy site near Goose Lake, west of Davis Creek, California, chromosome counts of 17 plants showed that, although in close proximity, the tetraploid and octoploid plants formed discrete patches (Fig. 3). While all were browsed severely by cattle at that site, those in the octoploid patch appeared taller and more vigorous, as contrasted with the smaller, more heavily damaged plants in the tetraploid patches. We found no plants at any of the mixed-ploidy sites with intermediate chromosome numbers suggestive of interploid hybridization.

Because individuals of *S. vermiculatus* show considerable vegetative plasticity, it is often difficult to distinguish tetraploid from octoploid plants in the field. However, as shown in

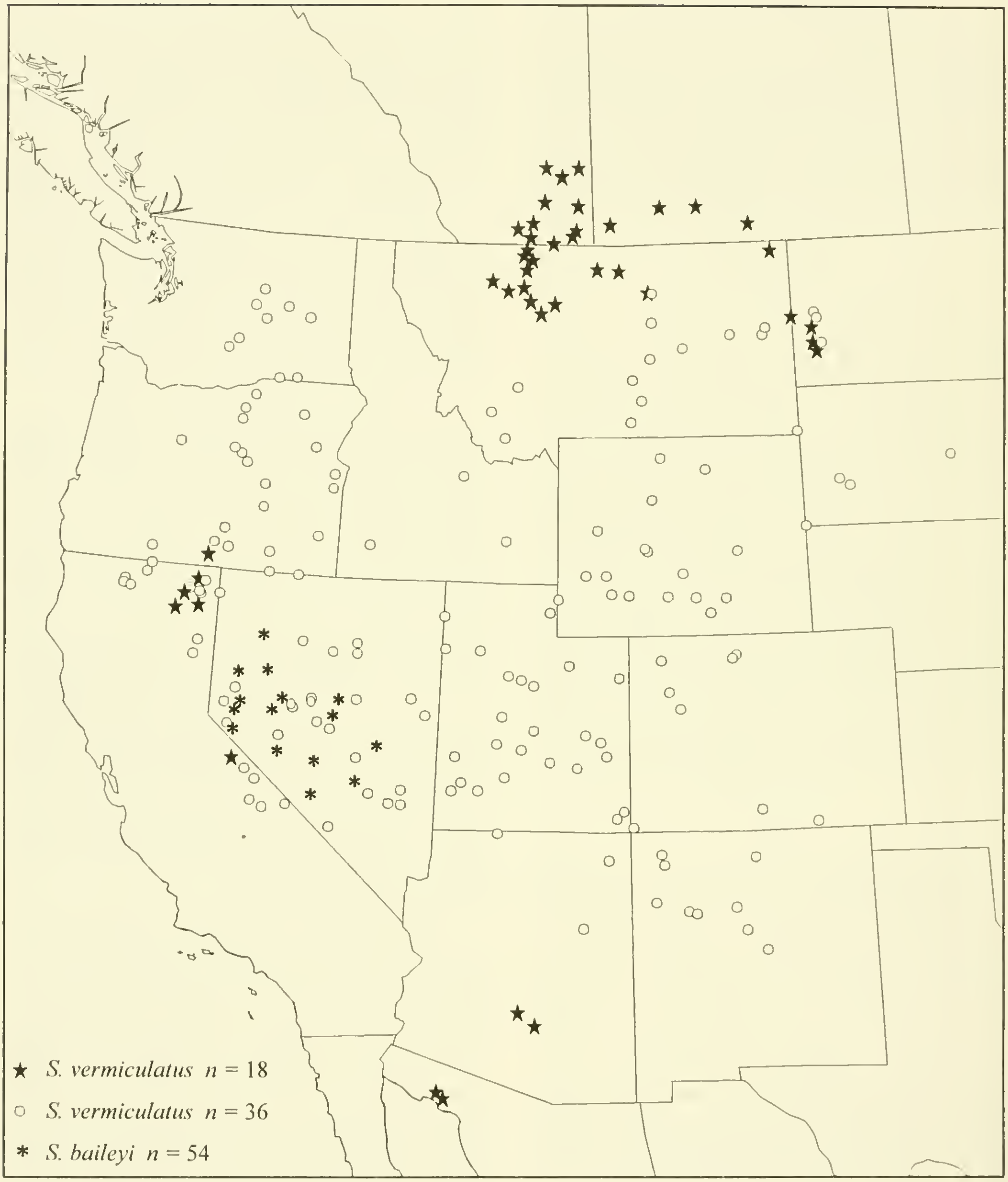


Fig. 1. Geographic distribution of chromosome counts for *Sarcobatus baileyi* and *S. vermiculatus*.

Table 1, the leaves of tetraploid plants are statistically shorter and narrower than those of octoploids.

Populations of octoploid *S. vermiculatus* may differ dramatically in stature (Roos 1984; Figs. 4, 5, Table 1), differences which are largely maintained in the common garden (Stutz unpublished data). However, only slight variation was encountered across larger geographical ranges. Plants from northern Oregon and Washington (the "northwestern 8x" group) were numerically tallest, though this was not statistically significant.

Inflorescence length showed few differences between ploidies or by geographic region in *S. vermiculatus*. However, temporal variation was observed which at a particular season gave the impression of geographic differences (data not

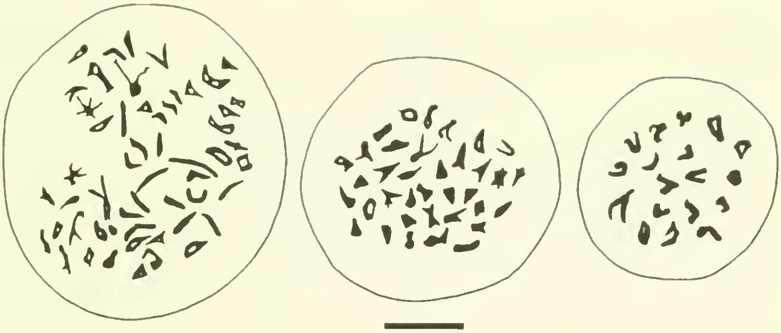


Fig. 2. Chromosomes of *Sarcobatus baileyi*, *n* = 54 (left), and *S. vermiculatus*, *n* = 36 (center) and *n* = 18 (right). Scale bar = 10 µm.

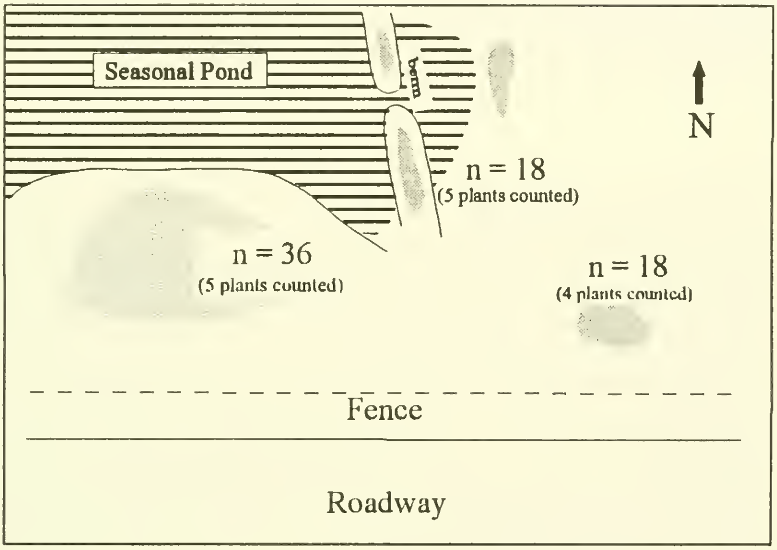


Fig. 3. Distribution of chromosome counts of *Sarcobatus vermiculatus* from 3.5 km west of Davis Creek, California, made in 1995. Three additional counts of 8x, 4x, and 4x (not shown), made the year previously, came from somewhere in the combined area of the 8x patch and the berm.

shown). Since we observed many populations both in early summer when meiotic buds were being collected, and later at the time when morphological measurements were taken, it was possible to compare inflorescences produced at these different times and observe differences that may have resulted from changes in season or weather. In early summer 1995, inflorescences of octoploid populations in northern California were very short compared to those observed elsewhere. However, as shown in Table 1, by late summer, at the time when measurements were taken, inflorescences were as long as or longer than those of other areas. Also, male inflorescences in some octoploid populations of northern Arizona and southern Utah were observed to be of normal size in early summer, but by measurement time were shorter (and much less abundant) than those of northern populations.

Male inflorescences of *S. baileyi* plants are consistently shorter than the shortest lengths of those of *S. vermiculatus* (Table 1). This was observed to be true both for young inflorescences, in which pollen mother cells were undergoing meiosis, and also in mature inflorescences after pollen had been shed. The plants of *S. baileyi* are generally also shorter

TABLE 1. Average of population means for *Sarcobatus baileyi* (SABA) and *S. vermiculatus* (SAVE) for morphological characters, measured in late summer, with standard error in parentheses. Column values within the same section that have a letter in common are not significantly different (SMM test).

	No. populations	Plant		Leaf		Male inflorescence
		Height (cm)	Width (cm)	Length (mm)	Width (mm)	Length (mm)
S. baileyi						
12x	5	53.7(3.83) b	133.3(33.51) bc	9.8(2.61) e	2.1(0.06) abc	4.3(0.15) d
S. vermiculatus						
Northern–4x	16	81.2(5.08) b	140.0(10.67) c	18.7(0.91) cd	1.9(0.06) bc	13.6(0.58) abc
Northern–8x	10	106.6(23.21) ab	149.4(23.49) bc	24.1(0.89) ab	2.2(0.07) ab	12.9(0.68) bc
Northwestern–8x	6	168.1(22.25) a	290.8(37.12) a	25.3(1.66) ab	2.4(0.14) a	14.9(1.09) abc
Central–8x	7	104.9(15.21) ab	187.6(32.08) abc	24.1(0.79) abc	2.1(0.04) abc	14.3(0.89) abc
Western–4x	5	134.2(9.68) ab	249.6(22.99) ab	25.6(3.13) ab	2.4(0.13) a	17.9(0.46) a
Western–8x	11	121.8(4.89) ab	238.5(13.31) ab	25.8(1.32) a	2.5(0.10) a	16.3(1.22) ab
Southern–4x	4	126.8(7.45) ab	215.1(17.41) abc	12.6(1.49) de	1.6(0.22) c	15.1(1.41) abc
Southern–8x	5	103.2(22.06) ab	196.8(33.93) abc	18.2(1.52) bcde	2.1(0.10) abc	11.0(1.67) c
SABA 12x Total	3	53.7(3.83) b	133.3(33.51) a	9.8(2.61) c	2.1(0.07) ab	4.3(0.15) b
SAVE 4x Total	25	99.1(6.20) ab	173.9(12.61) a	19.1(1.16) b	1.9(0.07) b	14.7(0.55) a
8x Total	39	119.6(8.38) a	209.2(13.40) a	24.0(0.65) a	2.3(0.05) a	14.2(0.53) a
SABA Total	3	53.7(3.83) b	133.3(33.51) a	9.8(2.61) b	2.1(0.07) a	4.3(0.15) b
SAVE Total	64	111.6(5.76) a	195.4(9.63) a	22.1(0.67) a	2.1(0.05) a	14.4(0.38) a

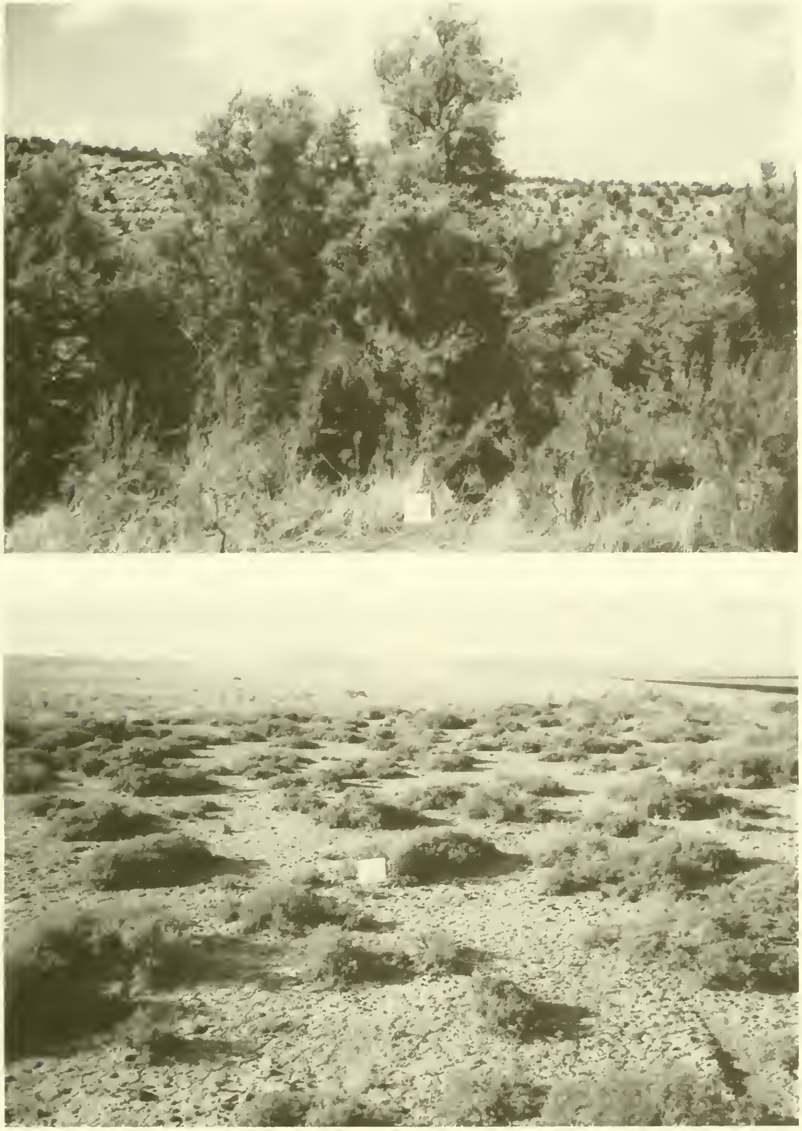
than those of octoploid *S. vermiculatus*, but are not significantly shorter than tetraploids using the present data set. Leaves of *S. baileyi* are shorter than those of either ploidy of *S. vermiculatus*, while not any narrower.

Although *S. baileyi* has been suspected to intergrade with *S. vermiculatus* (McMinn 1939), we found no morphological or cytological evidence for hybridization. *S. baileyi* was $n = 54$ throughout its range, but *S. vermiculatus*, even when growing nearby, was always $n = 36$. In locations where *S. vermiculatus* and *S. baileyi* come into contact, *S. baileyi* plants are often taller than usual, probably because of moister conditions, and conversely, *S. vermiculatus* plants become smaller and more spiny in drier circumstances, as they come near populations of *S. baileyi*. In spite of this convergence in stature, any confusion about their identity can be resolved when male inflorescences are present, and foliage characteristics are also often helpful. Besides the difference already noted in leaf length, leaves of *S. baileyi* are earlier-deciduous in the late summer than those of *S. vermiculatus*, and the time of appearance of new leaves in the spring usually differs, with *S. baileyi* leafing out first.

Sarcobatus baileyi flowers most profusely at leaf-flush, with male floral buds appearing terminally on new short shoots arising from the axils of woody branches. If conditions are favorable, a 2nd crop of inflorescences may be produced on the apices of elongate shoots. In *S. vermiculatus*, all flowering is on elongate shoots and may continue all summer when moisture is adequate (whether this relates to lowering of water tables through the season or to the exhaustion of surface moisture would be a matter for further study). Individual female flowers are usually located immediately below male inflorescences in both species.

As previously reported (Sanderson et al. 1988), the flavonoid complement of *Sarcobatus* species evidences the presence of an enzymatic activity for flavonol 6-oxygenation, with individual plants showing some or all of the 6-methoxy flavonols (6-methoxy kampferol, patuletin, and spinacetin), as well as the corresponding 6-unsubstituted flavonols (kampferol, quercetin, and isorhamnetin). In addition, 3-O-methylated flavonols were often observed.

S. baileyi plants from southeastern Nevada had flavonoids in proportions similar to those seen in *S. vermiculatus*, but samples from the western part of its range (western Nevada) showed a quantitatively different and more variable flavonoid profile, often with only small amounts of 6-methoxy compounds. We have not been able to discover morphological traits that correlate with this biochemical difference.



Figs. 4–5. Plants from tall- and short-statured populations of octoploid ($n = 36$) *Sarcobatus vermiculatus*: 4 (top), plant 2.5 m in height, about 10 mi north of Monticello, Utah; 5 (lower), plants 0.25 m in height, growing 10 mi north of Milford, Utah. Card is 20 × 20 cm.

DISCUSSION

Late Pleistocene and Holocene Distribution Patterns

Changes in altitudinal or geographic range were widespread among plants of western North America in response to fluctuating climates during the Pleistocene and Holocene (Betancourt et al. 1990). However, because of its apparent limitation to saline soils, *Sarcobatus* may be an example of a taxon with a range that did not shift extensively during these time periods.

Although long-distance eastward transport of small amounts of *Sarcobatus* pollen has been noted (Maher 1964, Birks 1981), more abundant stratigraphic occurrences would indicate that the genus was present locally (Thompson 1992), especially in the western or upwind parts of its species range. The presence of *Sarcobatus* pollen at near-full glacial or earlier is documented by longer pollen records from the

Columbia Basin in Washington (Barnosky 1985), eastern Idaho (Beiswenger 1991), northwestern Wyoming (Whitlock 1993), central Nevada (Thompson 1992), Owens Valley, California (Koehler and Anderson 1994), and northern Arizona (Anderson 1993). In addition, pollen or macrofossil records document the presence of *Sarcobatus* to at least the latest glacial in Arizona, Colorado, New Mexico, and Utah (Betancourt 1990). Early Holocene records of *Sarcobatus* have been reported from western Montana (Mack et al. 1983) and northeastern Wyoming (Markgraf and Lennon 1986). However, suitable sites for the preservation of Pleistocene pollen are few in the northern Great Plains (Ritchie 1987), resulting in a scarcity of information concerning Montana and the Dakotas, while Alberta and Saskatchewan were unavailable for occupation insofar as they were covered by the Laurentide ice sheet. Nevertheless, fossil evidence on the whole suggests that the range of occurrence of *Sarcobatus* was relatively little altered during glaciation.

It seems likely on ecological grounds, however, that the species *S. vermiculatus*, at least, was edaphically confined during the Pleistocene. In addition to saline geological strata, large evaporationally saline areas, such as the beds of desiccated Pleistocene lakes, have existed since early Holocene and presently form important habitats for *S. vermiculatus*. Most of these sites were nonsaline or submerged during times of glaciation. However, outcrops of saline geologic strata, which are particularly common in the Colorado Plateau and northwestern Great Plains, must have formed an acceptable habitat for *Sarcobatus* in the Pleistocene, much as they do at present.

Sarcobatus apparently persisted in the Great Basin and other areas through the climatic changes of the glacial/interglacial cycles of the Pleistocene. In the Great Basin during the last glacial maximum (ca 18,000 yr B.P.), trees and shrubs of the modern pinyon-juniper woodland of the Great Basin were forced well to the south, and bristlecone and limber pines grew 1000 m or more below their current limits, suggesting that temperatures were much cooler than today (perhaps 8–10°C for summer months; Thompson 1990). *Sarcobatus* and other halophytes apparently weathered these changes in climate and survived until the present in essentially the same locations they have apparently lived for many millenia.

Adaptive Advantages of Polyploidy

The absence of tetraploid *S. vermiculatus* within the Great Basin or other parts of the central species range (Fig. 1) might suggest that the tetraploid race in these areas has been replaced by competition from octoploids. In several other apparently autoploid complexes, polyploid members of the complex are more widespread than diploids (Manton 1934, Zohary and Nur 1959, Stutz et al. 1975, Stutz 1983), which is commonly true in other sorts of polyploid complexes as well (Babcock and Stebbins 1938, Stebbins 1950). The competitive superiority observed in polyploids may arise in part because of the effects of one-way introgression and multiple origin (Zohary and Nur 1959, Stebbins 1971, Soltis et al. 1993), both of which act to widen the genetic base and ecological amplitude of polyploids. Our morphological and flavonoid data suggest significant amounts of genetic variation existing within octoploid *S. vermiculatus* and 12-ploid *S. baileyi* that may have contributed to their adaptive success.

Mechanism of Chromosome Number Increase

Endosperm balance number and "triploid block" refer to a mechanism limiting the occurrence of polyploidy, to a greater or lesser degree, within various angiosperm taxa (Woodell and Valentine 1961, Johnston et al. 1980). In those where it is strongly operative, triploids (which could be derived from an unreduced gamete plus a normal gamete) are unable to survive through embryo development. Polyploidization, if any, must then follow other less favorable pathways, such as somatic doubling or the union of simultaneous unreduced gametes. Since the primary nutritive tissue within the Caryophyllales seed is perisperm (of nucellar origin) rather than endosperm (Cronquist 1988), limitation of polyploidy by endosperm balance is probably not to be expected within this order. Absence of restraint of polyploidization by the endosperm balance mechanism might thus be an additional reason for polyploidy prevalence within species of this group.

Our data on *Sarcobatus* suggest an absence of endosperm balance effects and the function of the single-unreduced gamete pathway. Octoploid populations contain rare 12-ploid individuals, probably derived by unreduced gametes

(4x + 8x = 12x) and apparent backcrosses of such to the parental chromosome number. Given sufficient selective value, a 12-ploid race like that of *S. baileyi* might be expected to eventually appear in *S. vermiculatus*.

Since the tetraploid chromosomal race should give rise to hexaploid plants by unreduced gametes in the same manner, the existence of an octoploid chromosomal race in the absence of any hexaploid race is therefore unexpected. This anomaly could be best explained if the tetraploid race were relatively old and had therefore become diploidized. In that case hexaploid individuals that might be formed would be functionally equivalent to triploids, and sterile. Therefore, if a race of higher ploidy was produced, it would have to be at the octoploid level or higher, as is observed.

Similar reasoning could be applied to polyploids in other taxa, for instance *Atriplex canescens* and *A. confertifolia* ($x = 9$) of the Chenopodiaceae. Both taxa exhibit widespread tetraploid races (Stutz and Sanderson 1979, 1983, Sanderson et al. 1990, Sanderson and Stutz 1994) and have formed polyploids at hexaploid or octoploid levels, which would provide an indication of whether the respective tetraploids are diploidized or not. In *S. vermiculatus* the absence of diploids and the failure of the tetraploid race to polyploidize to the hexaploid level both suggest that the tetraploid race is ancient, probably dating back into the Pleistocene.

Success of octoploid *S. vermiculatus* in the relatively southern parts of the species range, in comparison to tetraploid populations located along the U.S.–Canada border and in northeastern California, may suggest that octoploids are better adapted to warm, arid climates. If this is the case, their ascendency over the tetraploid race may therefore likely have occurred during the Holocene. The Sonoran tetraploid race occurs in a warmer climate, but it appears to be ecologically divergent and somewhat independent from the evolutionary trends of the remainder of the species.

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APPENDIX. Chromosome count localities for *Sarcobatus baileyi* and *S. vermiculatus*. Counts not showing a date for meiotic bud collection were made from root tips.

Ploidy	Plants counted	Nation, state, county: location	Date of meiotic bud collection
Sarcobatus baileyi			
12x	(1)	USA, NV, Churchill Co.: mi 48, US 50, 1 mi E of Sand Mountain turnoff	11 APR 96
12x	(1)	USA, NV, Churchill Co.: mi 76, US 50, due NW of Eastgate	11 APR 96
12x	(1)	USA, NV, Esmeralda Co.: county line, US 95, S side of Tonopa	15 APR 92
12x	(1)	USA, NV, Lander Co.: mi 1, NV 376, Big Smokey Valley, 15 mi S of US 50	15 APR 92
12x	(2)	USA, NV, Lander Co.: mi 11, NV 376, Big Smokey Valley	25 APR 95
12x	(1)	USA, NV, Lyon Co.: mi 11, NV 208, 5 mi E of Smith	12 APR 96
12x	(1)	USA, NV, Lyon Co.: mi 27, 15 mi N of Yerington	12 APR 96
12x	(1)	USA, NV, Lyon Co.: S side of Silver Springs	12 APR 96
12x	(2)	USA, NV, Mineral Co.: 5 mi S of Mina	24 APR 86
12x	(1)	USA, NV, Nye Co.: 5 mi N of Queen City Summit, NV 375	14 APR 92
12x	(1)	USA, NV, Nye Co.: mi 17, NV 379, S of Duckwater	11 MAY 88
12x	(3)	USA, NV, Nye Co.: NV 267-US 95 jct, Scotty's Junction	9 MAR 95
12x	(1)	USA, NV, Pershing Co.: 10 mi W of Sulphur	11 APR 91
12x	(2)	USA, NV, Pershing Co.: Toulon exit, I-80, 10 mi S of Lovelock	12 APR 96
12x	(3)	USA, NV, Washoe Co.: S-S ranch turnoff, N side of Wadsworth	12 APR 96
Sarcobatus vermiculatus			
4x	(3)	CAN, ALTA: 1.5 mi N of Warner	21 JUN 89, 29 JUN 91
4x	(2)	CAN, ALTA: 1 mi N of Aden	4 JUL 89
4x	(1)	CAN, ALTA: 2 mi E of Milk River	29 JUN 91
4x	(1)	CAN, ALTA: 5 mi N of Milk River	29 JUN 91
4x	(1)	CAN, ALTA: Dinosaur Provincial Park	5 JUL 83
4x	(1)	CAN, ALTA: N bank of South Saskatchewan River, Suffield Mil. Res.	—
4x	(2)	CAN, ALTA: Orion	JUL 85, 4 JUL 89
4x	(1)	CAN, ALTA: Pendant Orielle	4 JUL 89
4x	(2)	CAN, ALTA: Red Deer River coulee, N of Patricia	18 AUG 96
4x	(3)	CAN, ALTA: S of 41A jct on Prov. hwy 41, 5 mi E of Medicine Hat	1 AUG 95
4x	(1)	CAN, ALTA: Sandy Point	—
4x	(1)	CAN, ALTA: South Saskatchewan River, town of Bow River	5 JUL 83
4x	(3)	CAN, SASK: 1 km E of Meleval, Prov. hwy 13	26 JUL 96
4x	(3)	CAN, SASK: Big Muddy Valley, S of Bengough	27 JUL 96
4x	(5)	CAN, SASK: Cypress Lake, Prov. hwy 21	5 JUL 89, 1 AUG 95
4x	(3)	CAN, SASK: W Penteix access, Prov. hwy 13	26 JUL 96
4x	(2)	MEX, SON: RR km 193, 50 km W of Puerto Peñasco	7 SEP 92
4x	(4)	MEX, SON: RR km 222, 20 km W of Puerto Peñasco	13 SEP 95
8x	(1)	USA, AZ, Apache Co.: Many Farms	22 JUL 84
8x	(3)	USA, AZ, Coconino Co.: Fredonia	26 MAY 95
4x	(5)	USA, AZ, Maricopa Co.: Riggs Rd (Beltline) & 16th, 10 mi S of Phoenix	25 AUG 93
8x	(2)	USA, AZ, Navajo Co.: Holbrook	9 JUN 95
4x	(5)	USA, AZ, Pinal Co.: mi 140, AZ 287, 10 mi NW of Coolidge	13 SEP 95
8x	(3)	USA, CA, Inyo Co.: 10 mi NW of Bishop	18 AUG 94
8x	(3)	USA, CA, Inyo Co.: Big Pine	18 AUG 94
8x	(1)	USA, CA, Inyo Co.: Deep Springs Valley	18 AUG 94
4x	(3)	USA, CA, Lassen Co.: mi 13, 0.5 mi SW of Bieber	17 AUG 94, 9 JUN 95
8x	(1)	USA, CA, Lassen Co.: mi 89, US 395, 20 mi N of Litchfield	16 AUG 94
8x	(3)	USA, CA, Lassen Co.: Standish	16 AUG 94
4x	(3)	USA, CA, Modoc Co.: 0.5 mi W of Likely	16 AUG 94
4x	(11)	USA, CA, Modoc Co.: 2 mi W of Davis Creek	17 AUG 94, 5 AUG 95
8x	(6)	USA, CA, Modoc Co.: 2 mi W of Davis Creek	17 AUG 94, 9 JUN 95
8x	(2)	USA, CA, Modoc Co.: 7 mi W of Alturas	9 JUN 95
4x	(2)	USA, CA, Modoc Co.: Canby	17 JUL 94
4x	(2)	USA, CA, Modoc Co.: Centerville rd, 5 mi E of Canby	17 AUG 94
8x	(3)	USA, CA, Modoc Co.: E side of Alkali Lake, CA 299, Cedarville	17 JUL 94
8x	(3)	USA, CA, Modoc Co.: mi 13.75, US 395, 2 mi S of Alturas	10 JUN 95
8x	(3)	USA, CA, Modoc Co.: Modoc Wildlife Refuge, US 395, 5 mi S of Alturas	16 AUG 94
4x	(2)	USA, CA, Mono Co.: Bridgeport	18 AUG 94
8x	(2)	USA, CA, Mono Co.: N side of Mono Lake, CA 167	18 AUG 94
8x	(1)	USA, CA, Mono Co.: S of Benton	27 JUL 84
8x	(3)	USA, CA, Siskiyou Co.: 0.5 mi E of CA 161, US 97 jct, 3 mi NE of Dorris	17 JUL 94
8x	(2)	USA, CA, Siskiyou Co.: 3 mi S of Granada	9 JUN 95

8x	(3)	USA, CA, Siskiyou Co.: 4 mi E of Granada	9 JUN 95
8x	(2)	USA, CA, Siskiyou Co.: 5 mi S of Dorris	17 JUL 94
8x	(2)	USA, CA, Siskiyou Co.: Louie Rd., 0.5 mi E of I-5, 5 mi SW of Big Spring	9 JUN 95
ca. 9x	(1)	USA, CA, Siskiyou Co.: Louie Rd., 0.5 mi E of I-5, 5 mi SW of Big Spring	9 JUN 95
8x	(1)	USA, CO, Alamosa Co.: Alamosa	9 AUG 88
ca. 10x	(1)	USA, CO, Alamosa Co.: 5 mi W of Alamosa	9 AUG 88
8x	(3)	USA, CO, Garfield Co.: exit 87, I-70, Rifle	27 JUL 95
8x	(3)	USA, CO, Jackson Co.: 1 mi W of Walden	28 JUL 95
8x	(3)	USA, CO, Jackson Co.: 2 mi N of Hebron	28 JUL 95
8x	(3)	USA, CO, Las Animas Co.: Trinidad	7 MAY 96
8x	(2)	USA, CO, Mesa Co.: 4 mi W of Mack	27 JUL 95
8x	(6)	USA, CO, Moffat Co.: CO 318–county rd 21 jct, Little Snake River	10 JUL 95
8x	(1)	USA, CO, Montezuma Co.: Aztec Wash	18 MAY 88
8x	(3)	USA, CO, Rio Blanco Co.: 5 mi SW of Meeker, CO 13	27 JUL 95
8x	(3)	USA, ID, Bannock Co.: Hildreth St. gravel pit, Pocatello	12 JUL 95
8x	(1)	USA, ID, Custer Co.: mi 126, US 93, 15 mi N of Mackay	7 JUL 92
8x	(2)	USA, ID, Elmore Co.: ID 51 at N bank of the Snake River	13 JUL 95
8x	(1)	USA, MT, Beaverhead Co.: 6 mi E of Dell	14 JUN 88
ca. 10x	(1)	USA, MT, Beaverhead Co.: 6 mi E of Dell	14 JUN 88
4x	(1)	USA, MT, Blaine Co.: Ft. Belnap, S side of Milk River	5 JUL 89
8x	(1)	USA, MT, Carbon Co.: mi 18, US 310, 10 mi S of Bridger	15 JUN 88
8x	(1)	USA, MT, Carter Co.: 10 mi W of Alzada, US 212	29 JUL 92
4x	(3)	USA, MT, Cascade Co.: 5 mi N of Great Falls on Benton Lake rd	28 JUL 96
4x	(1)	USA, MT, Cascade Co.: Vaughn	4 JUL 85
8x	(3)	USA, MT, Dawson Co.: 15 mi NE of Glendive, MT 16	30 JUL 95
ca. 5x	(2)	USA, MT, Dawson Co.: Mikshako Park, Glendive	22 JUL 87
8x	(4)	USA, MT, Dawson Co.: Mikshako Park, Glendive	22 JUL 87, 30 JUL 95
8x	(1)	USA, MT, Fergus Co.: Charles M. Russell Wild. Refuge, S side of River	5 JUL 89
8x	(1)	USA, MT, Fergus Co.: mi 65, MT 19, S of US 191 jct, 40 mi E of Lewiston	5 JUL 89
8x	(2)	USA, MT, Garfield Co.: 30 mi E of Jordan	23 JUL 87
8x	(2)	USA, MT, Golden Valley Co.: 20 mi N of Lavina	3 JUL 85
8x	(1)	USA, MT, Golden Valley Co.: Lavina	3 JUL 85
4x	(1)	USA, MT, Hill Co.: Havre	31 AUG 85
8x	(2)	USA, MT, Jefferson Co.: Whitehall	24 JUL 87
4x	(1)	USA, MT, Judith Basin Co.: Geyser	3 JUL 85
8x	(2)	USA, MT, Madison Co.: Melrose	2 JUL 80, 7 JUL 85
8x	(2)	USA, MT, Petroleum Co.: 30 mi E of Winnett	23 JUL 87
4x	(2)	USA, MT, Phillips Co.: 10 mi S of Hays	5 JUL 89
8x	(2)	USA, MT, Phillips Co.: mi 6.5, MT 376, 10 mi S of Hays turnoff	5 JUL 89, 31 JUL 95
8x	(1)	USA, MT, Phillips Co.: mi 90, US 191, Charles M. Russell Wild. Ref.	5 JUL 89
4x	(2)	USA, MT, Richland Co.: 20 mi SE of Sidney, MT 16	22 JUL 87
4x	(3)	USA, MT, Sheridan Co.: 1 mi W of Plentywood	26 JUL 96
4x	(3)	USA, MT, Teton Co.: 1 mi S of Choteau	4 JUL 85, 23 JUN 89
4x	(3)	USA, MT, Teton Co.: Freezeout Lake, 5 mi N of Fairfield	4 JUL 85
4x	(1)	USA, MT, Teton Co.: Power turnoff, I-15	—
4x	(3)	USA, MT, Toole Co.: W side of Shelby	2 AUG 95
4x	(1)	USA, MT, Toole Co.: Marias River, I-15	4 JUL 85
4x	(2)	USA, MT, Toole Co.: mi 275, I-15, 10 mi N of Shelby	30 JUN 87
4x	(2)	USA, MT, Toole Co.: mi 282, I-80, 15 mi N of Shelby	4 JUL 85
4x	(3)	USA, MT, Toole Co.: Sunburst	4 JUL 85
8x	(3)	USA, MT, Yellowstone Co.: 10 mi N of Billings	3 JUL 85
4x	(2)	USA, ND, Billings Co.: 1 mi S of Medora-Fryburg Rd on East River Rd	25 JUL 96
4x	(5)	USA, ND, Billings Co.: 7 mi W of Fryburg	30 JUL 95, 25 JUL 96
8x	(1)	USA, ND, Billings Co.: 7 mi W of Fryburg	30 JUL 95
4x	(1)	USA, ND, Billings Co.: Theodore Roosevelt Natl. Park, S Unit	22 JUL 87
8x	(2)	USA, ND, Billings Co.: Theodore Roosevelt Natl. Park, S Unit	22 JUL 87
8x	(4)	USA, ND, McKenzie Co.: 0.5 mi N of Theo. Roosevelt NP, N Unit entrance, US 85	30 JUL 95
4x	(4)	USA, ND, McKenzie Co.: 10 mi W of Grassy Butte	30 JUL 95
8x	(3)	USA, ND, McKenzie Co.: mi 124, US 85, 4 mi S of Theo. Roosevelt entrance	25 JUL 96
8x	(1)	USA, NM, Bernalillo Co.: Prince & Rio Bravo, Albuquerque	22 MAY 96
8x	(2)	USA, NM, McKinley Co.: E side of Gallup	26 MAY 95
ca. 9x	(1)	USA, NM, McKinley Co.: E side of Gallup	26 MAY 95
8x	(2)	USA, NM, San Juan Co.: Navajo Mine	6 JUN 85, 25 JUL 85
8x	(3)	USA, NM, Sandoval Co.: San Ysidro	22 MAY 95
8x	(1)	USA, NM, Taos Co.: Ojo Calient	10 MAY 96
8x	(2)	USA, NM, Torrance Co.: Laguna del Perro, 5 mi E of Willard	9 MAY 96

12x	(1)	USA, NM, Torrance Co.: Laguna del Perro, 5 mi E of Willard	9 MAY 96
8x	(3)	USA, NM, Valencia Co.: Grants	26 MAY 95
8x	(3)	USA, NM, Valencia Co.: Laguna	26 MAY 95
8x	(1)	USA, NV, Churchill Co.: Middlegate	27 JUL 84
8x	(2)	USA, NV, Douglas Co.: mi 39, US 395, Carson Valley	5 AUG 95
8x	(1)	USA, NV, Elko Co.: 5 mi E of Carlin	23 JUN 82
8x	(2)	USA, NV, Elko Co.: 9 mi N of Montello	13 JUN 90
8x	(2)	USA, NV, Eureka Co.: 20 mi W of Eureka	11 MAY 89
8x	(1)	USA, NV, Eureka Co.: 8.5 mi W of NV 278, mi 40, 40 mi N of Eureka	15 AUG 94
8x	(1)	USA, NV, Eureka Co.: mi 45, NV 270, 10 mi N of Eureka (short statured)	13 JUL 95
8x	(2)	USA, NV, Humboldt Co.: 16 mi W of Winnemucca, NV 49	15 JUN 90
8x	(3)	USA, NV, Humboldt Co.: Denio	17 JUL 94
8x	(1)	USA, NV, Humboldt Co.: OR state line, McDermitt	14 JUN 90
8x	(1)	USA, NV, Lander Co.: 10 mi W of Austin	11 MAY 89
8x	(1)	USA, NV, Lander Co.: Battle Mountain	10 MAY 89
8x	(2)	USA, NV, Lincoln Co.: Caliente	30 MAY 86
8x	(2)	USA, NV, Lincoln Co.: Dry lake, 20 mi W of Caliente	20 APR 89
8x	(1)	USA, NV, Lincoln Co.: Panaca	27 JUN 86
8x	(1)	USA, NV, Lincoln Co.: Rachael	30 MAY 89
8x	(3)	USA, NV, Lyon Co.: mi 11, NV 208, 5 mi E of Smith	6 AUG 95
8x	(1)	USA, NV, Mineral Co.: 15 mi E of Hawthorne	23 APR 86
8x	(2)	USA, NV, Nye Co.: 10 mi N of Beatty	9 JUL 82
8x	(2)	USA, NV, Nye Co.: 20 mi NE of Ione	16 JUN 90
ca. 12x	(1)	USA, NV, Nye Co.: 20 mi NW of Tonopah towards Gabbs	21 APR 89
8x	(1)	USA, NV, Nye Co.: Gabbs	27 JUL 84
8x	(2)	USA, NV, Nye Co.: mi 103.5, 15 mi SW of Currant	11 MAY 88
8x	(3)	USA, NV, Washoe Co.: Wadsworth	6 AUG 95
8x	(2)	USA, NV, White Pine Co.: Cherry Creek	16 MAY 85
ca. 9x	(1)	USA, NV, White Pine Co.: Cherry Creek	16 MAY 85
8x	(1)	USA, NV, White Pine Co.: US 6/50, Spring Valley	16 MAY 85
8x	(2)	USA, OR, Baker Co.: Baker	14 JUL 94
8x	(3)	USA, OR, Grant Co.: 1 mi E of Dayville	3 AUG 95
8x	(3)	USA, OR, Grant Co.: mi 113, OR 19, 20 mi NW of Dayville	2 SEP 94
8x	(3)	USA, OR, Grant Co.: mi 37, US 395, 1 mi S of Silvies	4 AUG 95
8x	(2)	USA, OR, Harney Co.: 1 mi E of Burns, OR 78	4 AUG 95
8x	(3)	USA, OR, Harney Co.: Fields	18 JUL 94
8x	(3)	USA, OR, Jefferson Co.: Hay Creek, 2 mi S of Willowdale	16 JUL 94
8x	(2)	USA, OR, Klamath Co.: N side of Klamath Falls	17 JUL 94
8x	(3)	USA, OR, Lake Co.: Alkali Lake	17 JUL 94
8x	(3)	USA, OR, Lake Co.: mi 88, US 395, NE of Valley Falls	18 JUL 94
4x	(3)	USA, OR, Lake Co.: OR 140, W side of Lakeview	4 AUG 95
8x	(3)	USA, OR, Lake Co.: Plush	17 JUL 94
8x	(3)	USA, OR, Malheur Co.: 5 mi W of Vale	19 MAY 92
8x	(1)	USA, OR, Malheur Co.: Owyhee River Canyon, 5 mi W of Adrian	13 SEP 94
8x	(3)	USA, OR, Malheur Co.: Rome	18 JUL 94
8x	(1)	USA, OR, Morrow Co.: 1 mi SE of Lexington	1 SEP 94
8x	(3)	USA, OR, Morrow Co.: 0.5 mi NE of Ruggs (large statured)	3 AUG 95
8x	(2)	USA, OR, Umatilla Co.: 2 mi W of Stanfield	14 JUL 94
8x	(2)	USA, OR, Union Co.: Ladd Refuge, US 30, La Grande	14 JUL 94
8x	(2)	USA, OR, Wheeler Co.: 0.5 mi E of OR 207–OR 19 jct E of Spray	3 AUG 95
8x	(2)	USA, SD, Fall River Co.: Hat Creek, near Ardmore	6 JUN 89
8x	(1)	USA, SD, Lyman Co.: Cedar Creek, mi 146, SD 1806, 25 mi SE of Ft. Pierre	24 JUL 96
8x	(1)	USA, SD, Lyman Co.: Lower Brule	7 JUN 89
8x	(1)	USA, SD, Pennington Co.: 10 mi S of Wall	6 JUN 89
8x	(1)	USA, SD, Pennington Co.: SD 40, 0.5 mi S of Cheyenne River	29 JUL 95
8x	(3)	USA, UT, Duchesne Co.: Fruitland	10 JUL 95
8x	(1)	USA, UT, Emery Co.: US 6 exit, I-70, 5 mi W of Green River	11 MAY 84
8x	(1)	USA, UT, Emery Co.: 5 mi N of Woodside	25 JUL 85
8x	(2)	USA, UT, Emery Co.: Icelander Wash	—
6x	(1)	USA, UT, Emery Co.: Icelander Wash (mistake, broken cells?)	—
8x	(1)	USA, UT, Grand Co.: 1 mi E of Green River	—
8x	(2)	USA, UT, Grand Co.: 20 mi N of Moab	2 MAY 85
8x	(1)	USA, UT, Iron Co.: 3 mi S of Parowan	26 JUN 86
8x	(2)	USA, UT, Iron Co.: 5 mi N of Beryl Junction (short statured)	26 JUL 84
8x	(3)	USA, UT, Iron Co.: Lund (short statured)	26 JUN 84, 16 MAY 95
8x	(1)	USA, UT, Juab Co.: 5 mi NE of Scipio	26 JUN 86

8x	(1)	USA, UT, Millard Co.: 13 mi S of Deseret	30 MAY 89
8x	(1)	USA, UT, Millard Co.: 25 mi N of Milford (short statured)	30 MAY 89
8x	(2)	USA, UT, Millard Co.: USDA-FS Desert Exp. Sta., Pine Valley	24 MAY 94
8x	(3)	USA, UT, Rich Co.: mi 7, UT 16, 1 mi E of Woodruff	27 JUN 95
8x	(1)	USA, UT, San Juan Co.: 10 mi N of Hatch Trading Post	29 JUL 82
8x	(1)	USA, UT, San Juan Co.: mi 2, UT 262, 15 mi S of Blanding	12 MAY 84
8x	(3)	USA, UT, San Juan Co.: mi 82.5, US 191, 10 mi N of Monticello (large statured)	10 MAY 96
8x	(2)	USA, UT, Sevier Co.: 10 mi S of Fremont jct, I-70, on UT 72	20 JUN 84
8x	(1)	USA, UT, Sevier Co.: 5 mi W of Joseph	17 JUN 82
8x	(1)	USA, UT, Tooele Co.: town of Rush Valley	28 JUN 83
8x	(1)	USA, UT, Tooele Co.: E of Wendover	17 MAY 85
8x	(1)	USA, UT, Tooele Co.: Faust turnoff, mi 33, UT 36	17 MAY 85
8x	(1)	USA, UT, Tooele Co.: mi 51, I-80, E of Knolls	17 MAY 85
8x	(1)	USA, UT, Uintah Co.: 1 mi S of Bonanza	28 AUG 86
8x	(1)	USA, UT, Utah Co.: Fairfield	—
8x	(1)	USA, UT, Wayne Co.: 20 mi E of Notom	20 JUN 84
8x	(2)	USA, UT, Wayne Co.: mi 112, UT 24, 5 mi W of Hanksville	12 MAY 84
8x	(1)	USA, UT, Wayne Co.: N of Dirty Devil River at Hanksville	11 MAY 84
8x	(3)	USA, WA, Douglas Co.: WA 17-174 jct, 20 mi W of Grand Coulee	15 JUL 94
8x	(3)	USA, WA, Grant Co.: Moses Lake, Stratford rd, NE of airport	16 JUL 94
8x	(2)	USA, WA, Grant Co.: Soap Lake	15 JUL 94
8x	(3)	USA, WA, Lincoln Co.: 3 mi SW of Sprague on Sprague Lake rd	3 AUG 95
8x	(2)	USA, WA, Lincoln Co.: mi 103, WA 28, Lamona	16 JUL 94
8x	(2)	USA, WA, Walla Walla Co.: Touchet	14 JUL 94
8x	(3)	USA, WA, Walla Walla Co.: Walla Walla	3 AUG 95
8x	(2)	USA, WA, Yakima Co.: Granger	16 JUL 94
8x	(1)	USA, WA, Yakima Co.: WA 24-241 jct, near Hanford Reserve	16 JUL 94
8x	(3)	USA, WY, Big Horn Co.: N side of Greybull	28 JUL 95
8x	(1)	USA, WY, Carbon Co.: 13 mi S of Lamont	—
8x	(2)	USA, WY, Carbon Co.: 3 mi E of Rawlins	20 JUL 87
8x	(1)	USA, WY, Carbon Co.: Co. rd 402 exit, I-80, Elk Mtn.	20 JUL 87
8x	(3)	USA, WY, Carbon Co.: Saratoga	28 JUL 95
8x	(1)	USA, WY, Fremont Co.: Ice Slough, US 287, 15 mi W of Jeffery City	28 JUL 95
8x	(3)	USA, WY, Fremont Co.: Sweetwater Station	28 JUL 95
8x	(3)	USA, WY, Johnson Co.: exit 73, I-90, Crazy Woman Creek	29 JUL 95
8x	(1)	USA, WY, Lincoln Co.: Fontenelle Dam	17 JUN 88
8x	(1)	USA, WY, Lincoln Co.: Sage	18 JUN 93
8x	(1)	USA, WY, Natrona Co.: 5 mi N of Alcova	—
4x	(1)	USA, WY, Natrona Co.: Alcova (mistake, from broken cells?)	—
ca. 9x	(1)	USA, WY, Sublette Co.: 8 mi S of Boulder	3 JUL 85
8x	(1)	USA, WY, Sublette Co.: Pinedale	2 JUL 85
8x	(1)	USA, WY, Sweetwater Co.: 7 mi N of Rock Springs, US 187	19 JUN 80
8x	(1)	USA, WY, Sweetwater Co.: Farson	3 JUL 85
8x	(2)	USA, WY, Sweetwater Co.: Red Desert	20 JUL 87
8x	(1)	USA, WY, Sweetwater Co.: Rock Springs	2 JUL 85
8x	(3)	USA, WY, Washakie Co.: county line, 15 mi SW of Worland	28 JUL 95

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GEOGRAPHY OF EXOTIC PLANTS ADJACENT TO CAMPGROUNDS, YELLOWSTONE NATIONAL PARK, USA

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ABSTRACT.—Eleven campgrounds in Yellowstone National Park were studied to determine the geography of 10 specific exotic plant species adjacent to campgrounds. Exotics were found in only 6 campgrounds. Six species were found at Mammoth campground, a low-elevation, dry site with year-round use. Only 2 species were found in the other 5 campgrounds. Exotics decreased with distance from Mammoth campground out to 6 m and then increased, suggesting a spread in their distribution. Significant associations were found between exotic presence and both open and closed canopies and low levels of disturbance. Generally, exotics decreased with an increase in cover of other vegetation forms. Five species were found most frequently in big sagebrush habitat types.

Key words: exotic plants, campgrounds, disturbance, canopy cover, Yellowstone National Park.

Exotic plants have dramatically transformed vegetation of the western United States over the past century and can be found today in most disturbed wildlands. Their well-documented ability to displace native species is a primary concern regarding their presence in national parks (Marion et al. 1985, Mack 1986, Weaver and Woods 1986, Bedunah 1992, Cheater 1992, Kummerow 1992, Tyser and Worley 1992, Lesica and Ahlenslager 1993). The introduction and spread of exotic plants into national parks threatens the structure and functions of native plant communities. Previous studies have found exotics to be associated with road and trail disturbance, high light intensities provided by open canopies, and trampling in campsites (Dale and Weaver 1974, Cole 1981, Forcella and Harvey 1983, Kuss and Graefe 1985, Baker 1986, Cole and Knight 1990, Benninger-Truax et al. 1992, Tyser and Worley 1992).

In 1994, 140 exotic species were found in Yellowstone National Park, while in 1986 only 85 were known to occur there (Yellowstone National Park 1986; J. Whipple, Yellowstone National Park botanist, personal communication 1996). It was hypothesized that some of this increase might be related to activities within campgrounds. More exotics were expected to be found close to campgrounds where a source of seeds may have been introduced by humans, cars, and maintenance equipment; where ground disturbance had created areas that could serve as seedling establishment sites; and where the overstory canopy may have been opened for campsites. With that in mind, the objectives of this study were to determine whether exotics were distributed according to (1) distance from campgrounds, (2) amount of canopy (overstory) cover, (3) amount of disturbance, and (4) amount of ground cover.

STUDY AREA AND METHODS

We studied all 11 vehicle-accessible campgrounds of Yellowstone National Park, USA. The campgrounds (1820–2425 m elevation) occur within habitats ranging from big sagebrush/bluebunch wheatgrass (*Artemisia tridentata/Agropyron spicatum*) at lower elevations to subalpine fir/grouse whortleberry (*Abies lasiocarpa/Vaccinium scoparium*) at higher elevations (Table 1). Average annual precipitation near the 11 campgrounds ranges from 37 to 105 cm, and frost-free days range from 21 to 125 (Natural Resources Conservation Service 1994). Campgrounds range in age from approximately 30 to 78 yr. Overnight use today consists primarily of campers with automobiles and, secondarily, of hikers and bicyclists. While the type of use within campgrounds is relatively homogeneous, the number of campers varies substantially and is

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TABLE 1. Habitat types and related elevations and mean canopy covers in which exotic plants were found in Yellowstone National Park campgrounds.

Habitat type	Elevation range (m)	Campground(s)	Number of transects	Number of transects with exotics	Transect frequency (%)[a]	Exotic species found[b]	Mean canopy (%)[c]
Big sagebrush/blue bunch wheatgrass	1820	Mammoth	8	8	100	SK, YSC, HT, MULL, CT, DT	14
Big sagebrush/Idaho fescue	1895–2090	Slough Creek Pebble Creek	8	2	25	CT	0
Douglas-fir/common snowberry	1895–2000	Slough Creek Tower Fall	6	1	17	CT	0
Engelmann spruce/ sweetscented bedstraw or horsetail	1895–2090	Slough Creek Pebble Creek	7	1	14	CT	27
Subalpine fir/twinflower	2000	Tower Fall	3	0	0	none	n/a
Subalpine fir/pinegrass	2060–2275	Norris	21	2		OD, CT	
		Indian Creek			14		6
		Madison		1		CT	
Subalpine fir/grouse whortleberry	2075–2425	Canyon	35		9		
		Grant Village		1		CT	
		Norris					21
		Bridge Bay		2		CT	
		Lewis Lake					

[a] Transect frequency percentage of transects in a given habitat type that contain exotics.

[b] Key to exotic species found. SK = spotted knapweed, HT = hound's-tongue, CT = Canada thistle, OD = oxeye-daisy, DT = dalmatian toadflax, YSC = yellow sweetclover, MULL = common mullein.

[c] Mean canopy refers to quadrats in which exotics were found.

dependent on the number of sites within a campground and the length of time a campground is open (Wert 1994). Mammoth campground, located near the park's headquarters, is the only one open all year.

Ten exotic species were selected for study based on their designation by park staff as high priority for control (Yellowstone National Park 1986). These included spotted knapweed (*Centaurea maculosa*), hound's-tongue (*Cynoglossum officinale*), Canada thistle (*Cirsium arvense*), oxeye-daisy (*Chrysanthemum leucanthemum*), dalmatian toadflax (*Linaria dalmatica*), yellow sweetclover (*Melilotus officinalis*), Russian knapweed (*Centaurea repens*), musk thistle (*Carduus nutans*), tansy aster (*Tanacetum vulgare*), and common mullein (*Verbascum thapsis*). Species nomenclature and verification of alien status follow Hitchcock and Cronquist (1973). All species, except yellow sweetclover, are also considered noxious weeds by the states of Wyoming, Montana, or both. A noxious weed as defined by federal law is a plant of foreign origin that can directly or indirectly injure agriculture, navigation, fish and wildlife, or public health (Yellowstone National Park 1986, Bedunah 1992).

We systematically established 8 transects, with a random starting point, outward from and perpendicular to the edge of each campground. The edge was located where ≤10% vegetative cover existed adjacent to the campground road's outer border. To identify the distance at which exotic occurrence changed, we sampled contiguous quadrats (4 × 1 m) along each transect from just inside the campground edge (quadrat 0) to 15 m outside the edge (quadrat 15). Additionally, quadrats were sampled at 20, 25, 30, 40, and 50 m from the campground edge to determine the extent of occurrence at greater distances. Eight quadrats inside each campground and 8 control quadrats outside each campground were also sampled for comparisons. Data collected within each quadrat during summer 1994 included percent cover and density of exotics, percent canopy cover of trees and shrubs (using a spherical densiometer), percent cover of disturbance (disturbed bare ground, trampled grass, footprints, and social trails), and percent cover of bare ground and other vegetation. Additional data were collected and analyzed as reported by Allen (1996).

Distribution of exotic plant cover and density relative to distances from campground edges were displayed with side-by-side boxplots and scatterplots for campgrounds in which exotics were found. A Cox-Stuart test for trend (Daniel 1990) was used to determine the general trend in occurrence of exotics with increasing distance from the edge of Mammoth campground. Chi-square tests were used to determine whether significant associations existed between canopy cover and presence of exotics and between disturbance and presence of exotics ($\alpha = 0.05$ for all analyses).

RESULTS AND DISCUSSION

Species Distributions

Exotic plants were found in only 6 of 11 campgrounds (Mammoth, Slough Creek, Madison, Norris, Grant Village, and Bridge Bay). Six species were found at Mammoth (spotted knapweed, hound's-tongue, Canada thistle, dalmatian toadflax, yellow sweetclover, and common mullein). Canada thistle was found in all 6 campgrounds, while oxeye-daisy was found in just 1 quadrat at Norris campground. We observed no other exotics within the quadrats; however, we saw others in the vicinity.

Exotics and Distance from Campgrounds

Exotic plants at Mammoth campground were fairly numerous and occurred at all measured distances beyond the campground edge (Fig. 1). Few to no exotics were found within the quadrats placed immediately inside the campground edge (quadrats 0), due primarily to frequent and severe campground-associated disturbance. Exotic cover and density were higher immediately outside the campground edge (quadrats 1 and 2). Median exotic density and cover decreased from 2 m out to 4 m and 6 m, respectively, suggesting the campground may be a source of inoculation or introduction. This decrease in exotics with distance from disturbance is similar to results found by Dale and Weaver (1974), Benninger-Truax et al. (1992), and Tyser and Worley (1992). Beyond about 6 m, density and cover increased out to 9 m, and then became more variable. We found a general trend of higher density ($P = 0.001$) and cover ($P = 0.011$) at distances of 11–50 m (versus 0–10 m) from Mammoth campground edge. Canada thistle presence was

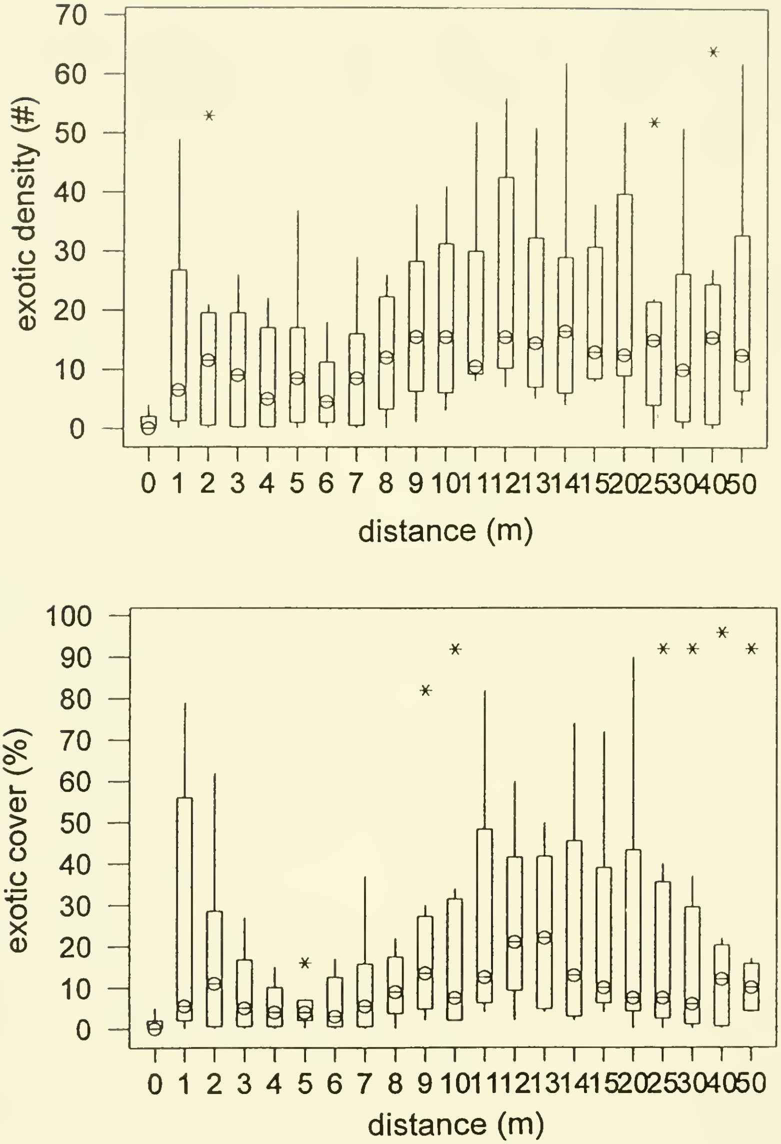

Fig. 1. Geography of exotic plants (density and cover) relative to distance from Mammoth campground edge.

highest between 11 m and 15 m, and between 30 m and 50 m, from campground edges, based on the cumulative relative frequency of Canada thistle relative to distance for all quadrats in which the plant was found. No decreasing trend in Canada thistle presence with distance was found.

Exotics and Canopy Cover

At Mammoth campground a significant association was found between canopy cover (at the 20% and 30% open/closed threshold divisions) and presence of hound's-tongue, spotted knapweed, and yellow sweetclover (Table 2). Hound's-tongue was significantly associated with closed canopies, suggesting the plant prefers or tolerates some degree of shade. It was more consistently found under higher canopy covers than any other exotic species (Fig. 2). This condition is similar to that reported by Lacey and Lacey (1986), where hound's-tongue was found in areas of

TABLE 2. Results of chi-square tests used to determine the association between canopy cover and exotic plant presence at Mammoth campground (*denotes significance at 0.05 level).

Exotic plant(s)	Canopy cover (%)	Chi-square	*P*-value
All	20	0.940	0.3323
	30	1.334	0.2481
	40	2.047	0.1525
Hound's-tongue	20	18.476	0.0000*
	30	5.483	0.0192*
	40	2.853	0.0912
Spotted knapweed	20	7.920	0.0049*
	30	3.859	0.0495*
	40	3.047	0.0809
Dalmatian toadflax	20	0.036	0.8495
	30	0.025	0.8744
	40	0.017	0.8963
Yellow sweetclover	20	19.313	0.0000*
	30	5.797	0.0161*
	40	3.053	0.0806
Mullein	20	2.098	0.1475
	30	2.208	0.1373
	40	1.743	0.1868
Canada thistle	20	0.355	0.5513
	30	0.173	0.6775
	40	0.137	0.7113

thick litter accumulation (as might be found under a forest with high canopy cover). Presence of spotted knapweed and yellow sweetclover was significantly associated with open canopy conditions (at the 20% and 30% open/closed threshold divisions). Spotted knapweed was always found under <20% canopy, and 75% of its occurrence fell below ≤5% canopy cover (Fig. 2). Previous studies have also found spotted knapweed to be more abundant under open canopies (Watson and Renney 1974, Losensky 1987, Milner 1995). Seventy-five percent of yellow sweetclover occurrences were beneath ≤10% canopy cover.

Dalmatian toadflax, found growing under a wide range of canopy covers, from 0% to 85%, was predominantly found under lower canopy cover values. While it is known to establish drier, open areas (Lajeunesse et al. 1993), results indicate its tolerance for moderate amounts of shade. Mullein was always found under a canopy cover of <30%, and 75% of its occurrences were under ≤5% canopy cover (Fig. 2). No significant association was found between canopy cover and mullein, nor between all exotics (when combined at Mammoth; Table 2), reflecting differences in canopy cover tolerance of individual species. In 84% of quadrats within which exotics were found, however, canopy cover was ≤30% (Fig. 2).

Eighty-seven percent of Canada thistle occurrences were under a canopy cover of ≤20%. Haderlie et al. (1989) found that warmth and long days favored Canada thistle growth. This condition is present in open canopy conditions during the Yellowstone National Park growing season. Although Canada thistle grows most often under open canopies, its occasional presence under more closed canopy covers (up to 95%) suggests it is somewhat tolerant of shade.

Exotics and Disturbance

Almost 40% of the quadrats at Mammoth contained no disturbance, and yet exotics were frequently encountered in these sites. In 75% of the disturbed quadrats at Mammoth, disturbance covered ≤20% of a quadrat. Presence of exotic plants at Mammoth was found to be significantly related to levels of disturbance of ≤20% ($P = 0.0002$). Exotics occurred most frequently at low disturbance covers partially because these are the conditions most commonly encountered at Mammoth. Higher disturbance covers (>60%) occurred infrequently and were usually found in the road edge disturbance of the 1st quadrat. Exotics were apparently less able to become established where disturbance levels were high.

Disturbance cover at Mammoth decreased from the campground edge out to a distance of 6 m. A general trend of decreasing exotic plant cover with increasing disturbance was found. In other studies it was often predetermined or assumed that disturbance decreased with distance from the road or trail, and that exotic presence decreased along this gradient (Weaver et al. 1989, Benninger-Truax et al. 1992). In this study the cover of disturbed ground was highest between 25 m and 40 m from Mammoth campground edge; however, highest exotic covers did not occur at comparable distances.

We found Canada thistle growing in all amounts of disturbance, although 20% of quadrats in which it was present had no evidence of disturbance. Canada thistle abundance increased as disturbance cover increased from 5% to 40%. No relationship was found between disturbance and Canada thistle when disturbance covers exceeded 60%. Where both Canada thistle and disturbance occurred, the

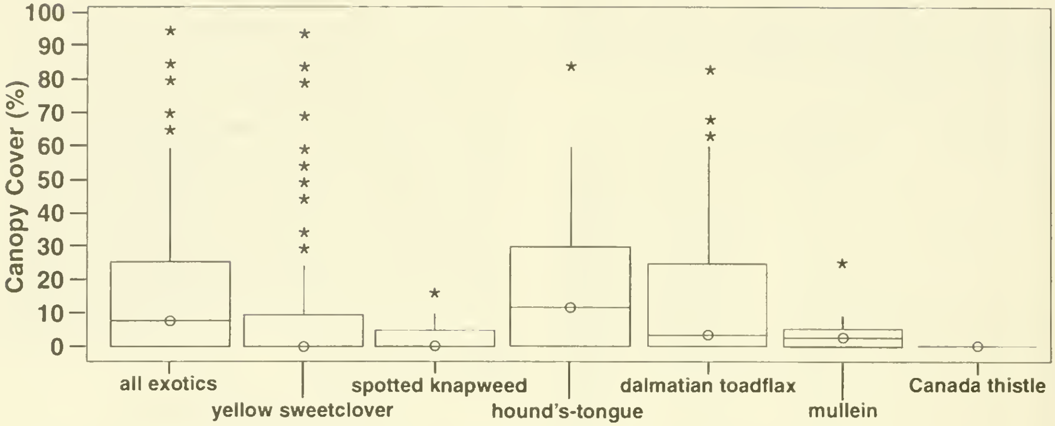

Fig. 2. Geography of canopy cover for all exotics—yellow sweetclover, spotted knapweed, hound's-tongue, dalmatian toadflax, mullein, and Canada thistle—where found at Mammoth campground.

plant was consistently rooted within the disturbance. The ability of Canada thistle to reproduce by lateral roots (Haderlie et al. 1989) may contribute to its presence in undisturbed and in both low and high levels of disturbed ground.

Patterns in exotic cover were explained, in part, by both canopy and disturbance. The highest exotic plant cover at Mammoth, in most transects, occurred where canopy and disturbance covers were both low. An exception to this occurred along 2 transects where a high percentage of hound's-tongue was found under canopies >25% (again indicating its tolerance of higher canopy covers).

Exotics and Other Vegetation

Exotic species were usually found growing with other plants, but overall the exotic plant cover at Mammoth decreased with an increase in individual covers of grasses, forbs, shrubs, and the combined cover of these vegetation forms. In contrast, 77% of Canada thistle occurrences were with at least 45% cover of other vegetation, and 33% of occurrences of Canada thistle were with ≥75% cover, suggesting Canada thistle can compete well for available resources. Overall, exotic cover was greatest where bare soil cover was ≤10%. When Canada thistle was present, bare soil always covered <40% of the quadrat. This result (more exotics where less bare soil is found) supports other results (reported above) for disturbance, as disturbance often produces bare soil. A slight decrease in exotic cover occurred with an increase in litter, and no relationship was found between exotic cover and that of moss/lichen, sedges, or trees.

Exotics and Habitat Type

Six exotic species were found in the big sagebrush/bluebunch wheatgrass habitat type, a lower-elevation, drier habitat type than others in Yellowstone (Table 1). Forcella and Harvey (1983) also found exotics to be common in low-elevation, dry habitats.

The abundance of exotics at Mammoth may be related to climate. Of all Yellowstone campgrounds, this site has the longest frost-free period (125 d) and the highest average temperatures (15.3°C) for the summer growing season (June–August; Natural Resources Conservation Service 1994). Spotted knapweed has been found to be more common at relatively low elevations (610–1829 m), and it requires 50–120 frost-free days (Chicoine et al. 1988, Milner 1995). Mammoth was the only campground that met these conditions.

Fewer exotic plants were found at higher elevations, perhaps due to shorter growing seasons, habitat types, and related higher canopy covers. Low temperatures have been shown to inhibit total germination and rate of germination in yellow sweetclover (McElgunn 1973). Oxeye-daisy is adapted to a more northern climate (Lindsay 1953) than that of Yellowstone National Park, perhaps explaining its presence at a higher elevation (2275 m) than most other exotics, in the subalpine fir/pinegrass habitat. Canada thistle was found in a wide range of habitats (big sagebrush/Idaho fescue, Douglas-fir/common snowberry, Engelmann spruce/sweetscented bedstraw, Engelmann spruce/horsetail, subalpine fir/grouse whortleberry, and subalpine fir/pinegrass habitats), a range of elevations (1820–2365 m), and on slopes ≤10%. No exotics were found in the subalpine fir/twinflower habitat.

Random and Control Quadrats

All 8 random quadrats sampled within Mammoth campground contained hound's-tongue, spotted knapweed, dalmatian toadflax, and yellow sweetclover. Canada thistle was found in 2 quadrats within Slough Creek campground. Control quadrats near Mammoth were the only ones that contained exotic plants. Five of these 8 contained dalmatian toadflax.

CONCLUSIONS

Results of this study provide new information about the (1) geography of exotics within Yellowstone National Park and (2) canopy conditions under which some exotics may grow. Exotic occurrence was limited adjacent to most of the park's campgrounds, but it was relatively high adjacent to Mammoth campground. Exotics decreased with distance from the campground edge, up to 6 m, and then increased. The large number of exotics found colonizing between 11 m and 50 m from Mammoth campground edge disturbance may be a result of several factors: availability of viable seed, habitat type, canopy cover, year-round use, and proximity to roads and trails. Distribution of exotics at Mammoth suggests that plants may spread outward from the campground area or from other nearby roads and trails. Canada thistle was the most prevalent species in all other campgrounds, covering a wide range of habitats.

Canopy cover and exotic occurrence were inversely related for most species; however, hound's-tongue, Canada thistle, and dalmatian toadflax were also found under more closed canopy conditions. Fewer exotics occurred as disturbance increased, and exotics were frequently encountered in areas of no disturbance. Because undisturbed or slightly disturbed ground is common under natural conditions, exotics can be expected to colonize these areas given a seed source and sufficient light and nutrients. Canada thistle was found, however, in all amounts of disturbance, suggesting that many areas are suitable for its establishment. Generally, exotics decreased with an increase in cover of other vegetation, perhaps due to increased competition for available nutrients, water, and light. Canada thistle appears to compete well, as indicated by its occurrence with high percentages of other vegetation.

Resource management activities in Yellowstone may have contributed to the geography of exotics as found in this study. Some spraying and pulling of exotics in campgrounds has occurred, but most control efforts have been concentrated along roadsides (J. Sweaney, North District Resource Management coordinator, Yellowstone National Park, personal communication 1996). Canopy cover within forested campgrounds of the park is being reduced as necessary to prevent "hazard trees" from falling. Although exotics were found adjacent to few campgrounds, and a relatively small number of species was found, there are indications that exotics are spreading. The results of this study may be applied to ecosystems similar to this national park and can serve as a baseline for evaluating human-induced changes elsewhere.

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HABITAT CHARACTERISTICS OF SMALL MAMMALS IN SOUTHEASTERN UTAH

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ABSTRACT.—We describe habitat characteristics of 8 small mammal species occurring in the Manti-LaSal National Forest in southeastern Utah. Thirty-seven grids across 7 vegetation types were sampled by live-trapping from May though October 1994 and 1995. Logistic regression models of habitat measurements correctly classified small mammal presence 36%–87% of the time. Except for 1 instance, 4 *Peromyscus* species present in a specific vegetation type were negatively associated with forb or grass cover. *Microtus montanus* was present primarily on mesas and was positively associated with tall tree and low shrub cover. *Neotoma mexicana* was present only in canyons and was found primarily in the pinyon-juniper (*Pinus edulis–Juniperus osteosperma*) vegetation type. *Tamias* spp. was present in all vegetation types. Our results allow better management of these species by providing greater understanding of their use of habitat within vegetation types.

Key words: rodents, small mammals, microhabitat use, Utah.

A knowledge of habitat relationships of a species is fundamental to understanding its conservation and management needs. General descriptions of geographic distribution among vegetation types are available for most small mammals. However, relatively little quantitative data on habitat relationships within different vegetation types are available upon which detailed management plans can be based (Morrison et al. 1998).

Understanding the ecology of small mammals assists in preserving local biodiversity. Furthermore, conservation of small mammals assumes added importance because of their use as food by some threatened species. For example, the 4 *Peromyscus* species captured in our study area (Sureda and Morrison 1998) are an important source of food for the federally threatened Mexican Spotted Owl (*Strix occidentalis lucida;* Ward and Block 1995). They are often used as an alternative food source when primary prey items, such as woodrats (*Neotoma* spp.), are in short supply (Ward and Block 1995). In this regard it is important to understand factors that influence the presence of these and other prey species in specific vegetation types.

Therefore, our objective was to describe habitat characteristics associated with small mammals within specific vegetation types in canyons and on mesas of the Manti-LaSal National Forest in southeastern Utah. These data will help resource managers better understand the distribution of rodents by vegetation type and, in addition, better manage for species of special concern.

MATERIALS AND METHODS

Our study occurred on the Monticello Ranger District of the Manti-LaSal National Forest, San Juan County, Utah. The area is considered part of the Canyonlands Section of the Colorado Plateau geographic province (Thornbury 1965:417, 426). Elevation ranges from approximately 1830 m to 2680 m. Our study focused on Texas, Hammond, and Dark canyons, as well as the mesas between them. Dark Canyon was surveyed only in 1995, whereas Texas and Hammond canyons were surveyed in both 1994 and 1995.

Four vegetation types occur in the canyons, as defined by the Monticello Ranger District of the U.S. Forest Service (USFS): (1) riparian, (2) mixed-mountain brush, (3) mixed-conifer, and (4) pinyon-juniper (B. Thompson, USFS, personal communication). The 3 dominant vegetative types on mesas between the canyons are (1) ponderosa pine (*Pinus ponderosa*) forest, (2) grass-forb/shrub, and (3) a mixture of

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aspen (*Populus tremuloides*) and ponderosa pine stands (referred to as mixed-aspen hereafter; Sureda 1996).

Climate within our study area is characterized as semiarid to arid with hot, dry summers. Precipitation and snowfall occur mainly from October to May. Further details on the study area are in Sureda and Morrison (1998).

Grid Establishment

In April 1994 we randomly established 8 trapping grids in Texas Canyon and 12 grids in Hammond Canyon. During a trapping period 1 grid was sampled within each of the 4 canyon vegetation types. Therefore, there were 2 trapping periods in Texas Canyon and 3 in Hammond Canyon. On mesas we established 15 trapping grids, thus representing 5 trapping periods consisting of 1 trapping grid within each of the 3 mesa vegetation types mentioned above. In May 1995 we placed 1 grid in the mixed-conifer and pinyon-juniper vegetation types in Dark Canyon. Only 1 trapping period in each season (see below) was conducted in Dark Canyon.

We randomly placed a grid within each vegetation type. Each grid on mesas was set in a 5 × 5 trapping station pattern. Canyon topography varied in width from approximately 100 m to 300 m; therefore, grids were modified slightly to fit the vegetation type and were irregular in shape (i.e., 6 × 4 [plus an additional trap] pattern). All trapping stations were separated by 15 m. We trapped a total of 37 grids.

Trapping

Live-trapping was conducted during summer (May–July) and fall (August–October) 1994 and 1995. Each trapping period ran for 4 nights and 3 days. We trapped only on nights around a new moon (O'Farrell 1974, Travers et al. 1988) and used 2 trap sizes to increase the probability of catching woodrats and to minimize potential bias against capturing larger mammals in the smaller traps. Within each grid, 13 trapping stations consisted of 1 extra-large Sherman trap (10 × 12 × 37 cm) and 1 large Sherman trap (7.6 × 8.2 × 22.9 cm), with the remaining 12 trapping stations consisting of 2 large Sherman traps.

All traps contained rolled oats, peanut butter, and batting (Davis 1982), and were set before sunset and checked at sunrise. Individuals were identified by toe clipping.

Habitat Sampling

A 10-m transect bisecting each trap location was randomly established to determine habitat characteristics. Cover of the following habitat characteristics was estimated using a point intercept sampling method (Bonham 1989) along each transect at 1-m intervals: bare ground, litter, gravel, rock, water, moss, lichen, log, stump, tree species (≥5 cm dbh), shrub species, forb, and grass; litter depth was recorded in millimeters. Vertical structure of live vegetation was recorded for foliage present in height categories (0–0.5, >0.5–1, >1–2, >2–5, >5–15, >15–30, and >30 m). A vertical pole was used to record touches of live foliage up to the >5–15 m category, and an ocular (sighting) tube was used for higher categories (Morrison et al. 1998:149).

Analyses

Analyses of habitat data were conducted for 8 species of small mammals: deer mouse (*Peromyscus maniculatus*), canyon mouse (*P. crinitus*), brush mouse (*P. boylei*), pinyon mouse (*P. truei*), montane vole (*Microtus montanus*), Mexican woodrat (*Neotoma mexicana*), least chipmunk (*Tamias minimus*), and Colorado chipmunk (*T. quadrivittatus*). Species with <10 captures for a particular vegetation type were excluded from further analysis in that type.

We evaluated relationships between small mammal numbers (total captures) and habitat variables by seasons (summer, fall) and years, using a multivariate analysis of variance (MANOVA; $P < 0.05$; Zar 1984:244–251). A MANOVA was conducted to determine if data could be combined over seasons and years in subsequent analyses. Because only 2 of 30 comparisons had significant ($P < 0.05$) year-by-season interaction (Sureda 1996), each species' numbers were combined over years and seasons in a stepwise logistic regression analysis.

To determine which habitat variables might predict the presence or absence of a species within each vegetation type, a stepwise logistic regression (Hosmer and Lemeshow 1989: 87–88) was conducted for each species in each vegetation type. Logistic regression is a 2-group, nonparametric analysis similar to discriminant analysis. Logistic regression models identified those variables primarily responsible for separating used trap sites from nonused trap sites. The criterion for inclusion of a variable in the logistic regression model was $P < 0.10$. Wald chi-square (Hosmer and Lemeshow 1989: 16–17) was then used to evaluate variables selected by the logistic regression model to determine final model significance. A classification table was calculated that summarized the ability of each model to correctly separate used from nonused traps.

Sample sizes were highly unequal between traps at which a species was captured (used traps) and traps where the species was not captured (nonused traps). Therefore, we initially ran each logistic regression analysis by randomly selecting habitat characteristics from 30 nonused traps to compare with data for used traps so that comparisons were more equal in sample size. Habitat variable(s) that occurred in >20% of the 30 models (for each species in each vegetation type) were force entered into a final logistic regression model. The model with the final variables was used to describe habitat features associated with presence or absence of a small mammal species in a particular vegetation type. Thus, we present species-specific descriptions of distribution across vegetation types and discuss variables apparently responsible for determining species presence.

RESULTS

Cover of forbs, rocks, litter, and evergreen and deciduous shrubs appeared in most logistic regression models for the small mammal species analyzed (Table 1). Note, however, that use of a specific habitat variable sometimes varied substantially for a species between vegetation types. For example, presence of deer mice was negatively associated (i.e., use less than abundance) with forbs in the mixed-aspen vegetation type, but positively associated with forbs in mixed-mountain brush; and presence of montane voles was positively associated with deciduous shrubs in mixed-aspen, but negatively associated with deciduous shrubs in grass-forb/shrub.

The deer mouse was present in all vegetation types. Correct classification rates for its presence in specific vegetation types ranged from 39% in pinyon-juniper to 79% in mixed-aspen (Table 2). The canyon mouse was captured primarily in canyons; correct classification ranged from 58% in mixed conifer to 76% in riparian vegetation (Table 2). The brush mouse also was captured primarily in canyons. Correct classification ranged from 63% in mixed-conifer to 75% in mixed-mountain brush (Table 2). The pinyon mouse, captured primarily in pinyon-juniper, was negatively associated with low deciduous shrubs (Table 1).

The montane vole was captured primarily on mesas; correct classification was 71% in mixed-aspen and 87% in grass-forb/shrub (Table 2). In mixed-aspen its presence was positively associated with tall deciduous trees and with low deciduous shrubs. In grass-forb/shrub its presence was negatively associated with low deciduous and positively associated with low evergreen shrubs (Table 1).

The Mexican woodrat was captured only in canyons. This species was captured primarily in pinyon-juniper, where its presence was correctly classified 65% of the time. It was negatively associated with canopy cover and positively associated with cacti and rock cover. In mixed-mountain brush its presence was correctly classified 60% of the time (Table 2), and it was positively associated with low evergreen and deciduous shrubs (Table 1).

The least chipmunk was captured in all vegetation types, and correct classification for its presence ranged from 36% in mixed-mountain brush to 84% in mixed conifer (Table 2). The Colorado chipmunk was primarily captured in canyons; correct classification ranged from 58% in mixed conifer to 86% in riparian (Table 2).

DISCUSSION

Most models we developed were good predictors (i.e., correct classification >60%) of the presence of small mammals. This was largely due to the similarity in patterns of habitat use for most species between years (see Methods).

Our study showed, however, the complicated distribution of animals among vegetation types in the same geographic area; there was little commonality in habitat variables selected *among* vegetation types for any species. Thus, gross generalizations of habitat use are inadequate for site-specific management of these species. Our models may be used to predict the response of species to proposed

TABLE 1. Used and nonused habitat variables included in logistic regression models for small mammal species within vegetation types, Manti-LaSal National Forest, San Juan County, Utah. The criterion for inclusion of a variable in the logistic regression model was $P < 0.10$.

Species Vegetation type Grouped variable	Used		Nonused	
	$\bar{x}$	s	$\bar{x}$	s
Peromyscus maniculatus				
Mixed-aspen (165/250)[a]				
Forb cover	15.3	13.09	20.0	18.09
Evergreen trees >15–30 m	5.0	15.27	11.9	20.91
Ponderosa pine (148/250)				
Canopy cover	26.8	25.60	38.7	24.43
Grass-forb/shrub (152/250)				
Grass cover	7.1	16.82	4.2	12.04
Evergreen shrubs <0.5 m	28.7	21.55	17.9	17.09
Pinyon-juniper (135/275)				
Rock cover	5.8	9.64	7.3	12.45
Deciduous shrubs <0.5 m	13.8	21.09	9.2	14.82
Mixed-conifer (161/275)				
Litter depth	27.0	14.21	32.9	19.73
Evergreen trees >15–30 m	3.6	9.91	10.9	20.36
Mixed-mountain brush (167/250)				
Forb cover	11.1	12.82	7.1	10.64
Rock cover	1.9	5.82	4.7	10.18
Riparian (146/250)				
Evergreen trees >1–2 m	3.8	8.04	6.1	10.36
P. crinitus				
Pinyon-juniper (65/275)				
Rock cover	14.0	14.82	6.9	10.91
Deciduous shrubs >1–2 m	16.9	17.36	9.4	13.91
Mixed-conifer (31/275)				
Forb cover	2.9	8.64	6.4	9.73
Rock cover	5.3	12.45	0.0	0.00
Evergreen shrubs <0.5 m	10.0	12.55	3.5	8.09
Evergreen shrubs >0.5–1 m	2.9	6.36	0.5	0.45
Deciduous shrubs >1–2 m	5.9	10.09	12.5	17.45
Mixed-mountain brush (51/250)				
Grass cover	3.1	7.04	9.6	12.18
Forb cover	2.3	5.03	9.8	12.18
Rock cover	7.3	9.89	3.0	6.15
Riparian (38/250)				
Litter depth	13.3	18.62	22.2	23.04
P. boylei				
Grass-forb/shrub (19/250)				
Litter cover	81.8	15.73	65.5	21.36
Pinyon-juniper (98/275)				
Bare ground cover	32.4	21.64	39.4	22.18
Mixed-conifer (60/275)				
Grass cover	2.3	5.73	5.5	10.91
Rock cover	3.5	7.09	5.9	13.64
Evergreen trees >2–5 m	24.7	24.82	30.8	29.82
Evergreen trees >5–15 m	16.6	26.03	23.0	30.00
Mixed-mountain brush (56/250)				
Grass cover	3.1	7.03	9.6	12.18
Forb cover	2.3	5.04	9.8	12.18
P. truei				
Pinyon-juniper (73/275)				
Deciduous shrubs >1–2 m	5.5	9.91	11.3	15.18

TABLE 1. Continued.

Species Vegetation type Grouped variable	Used		Nonused	
	$\bar{x}$	s	$\bar{x}$	s
Microtus montanus				
Mixed-aspen (62/250)				
Deciduous trees >15–30 m	22.0	26.73	10.9	22.36
Deciduous shrubs <0.5 m	30.8	22.18	19.1	21.36
Grass-forb/shrub (30/250)				
Evergreen shrubs <0.5 m	38.5	18.45	23.8	20.55
Deciduous shrubs >0.5–1 m	1.8	5.01	12.1	15.73
Neotoma mexicana				
Pinyon-juniper (23/275)				
Cactus cover	2.7	4.27	1.2	3.55
Rock cover	12.6	11.18	7.6	11.73
Canopy cover	3.4	5.53	8.4	11.40
Mixed-mountain brush (10/250)				
Evergreen shrubs <0.5 m	13.6	16.18	5.1	10.36
Deciduous shrubs >1–2 m	62.7	31.64	39.2	26.09
Tamias minimus				
Mixed-aspen (96/250)				
Evergreen trees >2–5 m	6.7	14.36	12.8	22.45
Deciduous trees >5–15 m	19.7	27.91	13.5	20.91
Deciduous shrubs >2–5 m	8.0	16.91	3.8	11.00
Ponderosa pine (70/250)				
Rock cover	4.8	9.27	2.3	6.36
Canopy cover	27.9	24.83	35.7	25.45
Grass-forb/shrub (131/250)				
Grass cover	8.1	10.82	20.6	27.45
Pinyon-juniper (35/275)				
Litter cover	61.0	26.09	45.1	26.55
Litter depth	26.6	18.86	16.8	15.97
Deciduous shrubs <0.5 m	20.0	23.00	9.7	16.18
Mixed-conifer (49/275)				
Rock cover	1.8	4.55	6.1	13.64
Mixed-mountain brush (25/250)				
Evergreen trees >1–2 m	10.5	17.18	6.0	14.27
Riparian (23/250)				
Forb cover	3.2	6.45	9.0	12.01
Litter depth	32.2	18.76	20.7	22.86
T. quadrivittatus				
Pinyon-juniper (56/275)				
Rock cover	15.7	15.09	6.8	10.91
Litter depth	9.8	8.13	18.6	16.92
Deciduous shrubs >1–2 m	16.4	17.09	9.6	14.18
Mixed-conifer (36/275)				
Litter cover	60.8	34.00	77.9	24.55
Rock cover	15.4	23.64	4.8	11.45
Deciduous shrubs >2–5 m	1.0	2.91	5.8	13.27
Mixed-mountain brush (28/250)				
Forb cover	2.6	4.91	8.8	11.73
Litter depth	18.4	12.51	33.8	18.56
Riparian (22/250)				
Litter depth	6.5	5.56	22.2	23.11
Deciduous trees >1–2 m	1.3	3.18	10.5	16.09

[a] Sample sizes in parentheses (*n* used traps/*n* trap locations).

TABLE 2. Percentage of samples correctly classified by logistic regression for presence and absence of rodents by vegetation type, Manti-LaSal National Forest, San Juan County, Utah.

	Mesas			Canyons			
Species	Mixed-aspen	Ponderosa pine	Grass-forb/shrub	Pinyon-juniper	Mixed-conifer	Mixed-mountain brush	Riparian
Peromyscus maniculatus	79/41[a]	63/55	67/46	39/72	78/35	53/65	75/30
P. boylei	p[b]	np[c]	74/63	65/53	63/58	75/68	np
P. crinitus	np	p	np	63/68	58/81	71/67	76/47
P. truei	np	p	p	69/51	p	np	np
Microtus montanus	71/68	p	87/53	p	p	p	p
Neotoma mexicana	np	np	np	65/74	p	60/70	p
Tamias minimus	48/64	54/67	75/48	63/86	84/20	36/80	61/61
T. quadrivittatus	np	np	p	77/64	58/67	79/54	86/55

[a] Values are percent correctly classified for presence/absence of species.

[b] p = species present, but sample size insufficient for analysis.

[c] np = species not present.

changes in habitat conditions (e.g., changes in tree density caused by timber management or prescribed fire).

Deer mice in canyons were more abundant in all vegetation types than the other 3 more specialized *Peromyscus* species captured (see also Sureda and Morrison 1998). In contrast, Fitzgerald et al. (1994) noted that *P. maniculatus* were locally scarce or absent where other habitat-specific *Peromyscus* species occur. However, Armstrong (1979) noted that it is not uncommon for *Peromyscus* species to co-occur in areas where vegetation is heterogeneous, as is found within canyons in our study area. For example, our trapping grids in the mixed-conifer vegetation type within canyons had scattered pinyon pines or patches of shrubs within them. Overall, our results corroborate the literature that describes the deer mouse as a generalist, inhabiting a wide range of vegetation types in North America (Burt and Grossenheider 1976, Hoffmeister 1986, Fitzgerald et al. 1994).

Logistic regression models of the canyon mouse for mixed-conifer, pinyon-juniper, and mixed-mountain brush vegetation types show that canyon mouse presence was positively associated with rock cover. This habitat characteristic is consistent with the literature that describes rocky, slickrock, and cliff habitats associated with this species (Hoffmeister 1986, Johnson and Armstrong 1987, Fitzgerald et al. 1994). Johnson and Armstrong (1987) noted that vegetation in an area may have little or no effect on local distribution of this species, but that the species is associated with the rocky substrate of an area rather than the plant association.

Models of the brush mouse indicate an association with open areas; measures of tree and shrub cover either did not enter, or showed a negative association, in the models. However, the species is characteristically associated with rough, broken terrain with boulders and heavy brush (Wilson 1968, Hoffmeister 1986, Fitzgerald et al. 1994). Therefore, our results appear to contradict the literature, with brush mice occurring in less sparsely vegetated areas than are typical elsewhere. Our results for the pinyon mouse compare favorably with results of others (Wilson 1968, Burt and Grossenheider 1976, Armstrong 1979, Hoffmeister 1986, Fitzgerald et al. 1994).

The mixed-aspen vegetation type on mesas is characteristic of habitat in which the montane vole is usually found (Hoffmeister 1986, Fitzgerald et al. 1994). Snowberry (*Symphoricarpos rotundifolius*) is the predominant species in the deciduous shrub group and may be an important source of food and cover to the montane vole. The grass-forb/shrub vegetation type in our study area, although not typical of montane vole habitat as described in the literature, was consistently used by this species. The evergreen shrub species was dominated by sagebrush (*Artemisia tridentata*), which may be used for food or cover.

In the Mexican woodrat model for the pinyon-juniper vegetation type, variables positively associated with its presence are consistent with the rocky habitat described for this species (Burt and Grossenheider 1976). Armstrong (1979), Cornely and Baker (1986), and Fitzgerald et al. (1994) also reported the Mexican woodrat is associated with pinyon-juniper woodlands. In the mixed-mountain brush model, the Mexican woodrat was positively associated with evergreen and deciduous shrubs. The evergreen shrub group was interesting in that the predominant representative of the group was Oregon grape (*Berberis repens*), which might be an important source of food and cover. Here, however, rocky substrates were not identified to be of primary importance for woodrat presence.

Models for the least chipmunk are varied and show both positive and negative associations with similar variables in different vegetation types. Fitzgerald et al. (1994) noted that the least chipmunk ranges over a wide area and in many different vegetation types including semidesert shrublands, montane woodlands and shrublands, and forest edge. Within this range of vegetation, Fitzgerald et al. (1994) noted that the least chipmunk occupies relatively open sunny areas on the edge of escape cover.

In all models the Colorado chipmunk was negatively associated with litter cover, and in 2 vegetation types it was positively associated with rock cover. The Colorado chipmunk is typically associated with broken terrain and canyons, as well as with open, rocky, brushy areas (Lechleitner 1969, Fitzgerald et al. 1994). In our study this species was most abundant in the pinyon-juniper vegetation type (see also Sureda and Morrison 1998), which corroborates with Lechleitner (1969), who also found the Colorado chipmunk in pinyon-juniper forests. Best et al. (1994) found that woodlands represent 36% of the areas occupied by this species.

To develop management conservation guidelines for a given species, one must know in some detail what constitutes habitat for the species; management at this microscale is difficult. Our results can, however, be used to predict how management actions will positively or negatively influence the presence of each species by vegetation type. Such analyses may be important in designing site-specific land-use plans for both the preservation of biodiversity and the enhancement of individual species of concern.

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PREDATORY BIRD POPULATIONS IN THE EAST MOJAVE DESERT, CALIFORNIA

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ABSTRACT.—We surveyed 7 species of predatory birds weekly during a 12-month period (December 1992 through November 1993) in the east Mojave Desert, California. The Common Raven (*Corvus corax*) was the most frequently observed species with an average of 6.9 sightings per 100 km. Turkey Vultures (*Cathartes aura*), Red-tailed Hawks (*Buteo jamaicensis*), Loggerhead Shrikes (*Lanius ludovicianus*), American Kestrels (*Falco sparverius*), Golden Eagles (*Aquila chrysaetos*), and Prairie Falcons (*Falco mexicanus*) were seen in decreasing order of frequency of observation through the study period. Ravens, Red-tailed Hawks, Loggerhead Shrikes, American Kestrels, and Prairie Falcons were seen throughout the year. Turkey Vultures were not present during winter months, while Golden Eagles were seen only during November and December. Turkey Vultures, Red-tailed Hawks, and ravens were most numerous on agricultural lands, while Loggerhead Shrikes were most common at urban areas. Raven numbers increased with increasing number of linear rights-of-way parallel to the survey route. Perching was the most common behavior type, although Turkey Vultures and ravens were often observed soaring, flying, or standing on the ground near highways. Transmission powerline towers and telephone poles were used as perch sites disproportionately to availability.

Key words: Mojave Desert, predatory birds, perch sites, year-round surveys.

Information on annual variations in the composition of predatory bird communities in temperate environments may be useful in conservation planning, and yet these variations are seldom measured (Newton 1979, Eakle et al. 1996, Rodríguez-Estrella et al. 1998). For example, in the Mojave Desert of California there is little information regarding year-round presence and abundance of predatory birds, although a variety of these species are (1) viewed as important (eagles, hawks, falcons), (2) experiencing population declines (Loggerhead Shrike [*Lanius ludovicianus*], Small 1994; Prairie Falcon [*Falco mexicanus*], Boyce 1986), or (3) allegedly endangering threatened wildlife (Common Raven [*Corvus corax*], Boarman 1993). Between December 1992 and November 1993, we conducted weekly surveys of 7 species of predatory birds over a portion of the eastern Mojave Desert in California. Our purpose was to collect information that might serve as baseline data for wildlife assessments following inevitable changes in land use (e.g., decreased grazing, increased recreation, increased residential development).

STUDY SITE AND METHODS

Our study site in San Bernardino County, California (115°45′E, 34°33′N), is bounded on all sides by mountain ranges (Fig. 1). The northern boundary is the Bristol, Granite, and Providence Mountains; the eastern boundary is defined by the Old Woman Mountains; the southwest border is the Bullion Mountains; and the southern portion of the study area is the Calumet and Sheep Hole Mountains. The Cadiz Valley occupies the southeastern portion of the study area, and Fenner Valley is in the northeast. Our study area comprises a variety of habitats including unvegetated dry lake beds, creosote (*Larrea tridentata*) scrub, and mixed desert scrub communities on the dry, relatively low mountain ranges of the area (Vasek and Barbour 1977). The climate is seasonal, warm (>26°C) in summer and cool (<11°C) in winter, with an annual mean temperature of 17°C ± 9°C (*s*). Average rainfall is <12 cm, with most precipitation occurring between December and March (Johnson 1968).

We surveyed 7 species of predatory birds weekly from an automobile over a 12-month

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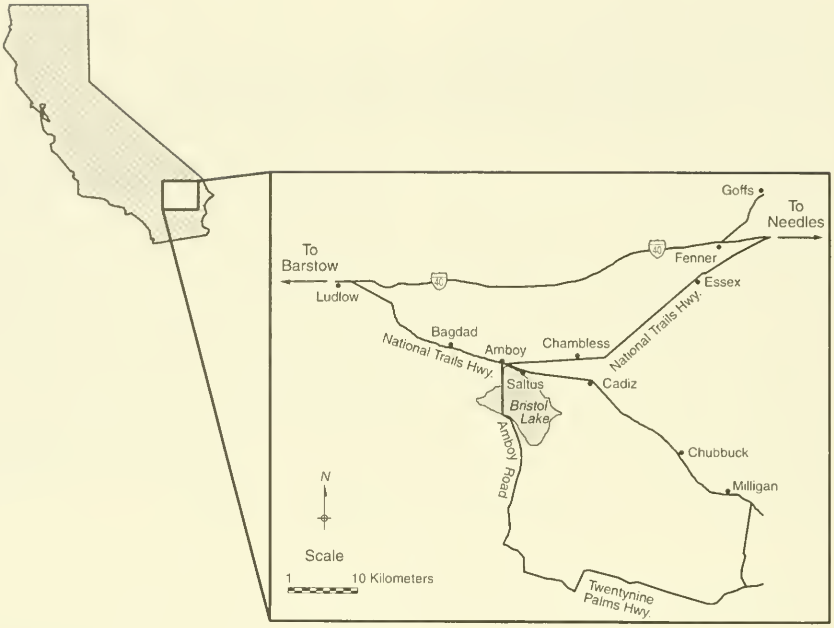

Fig. 1. Study area showing survey route, east Mojave Desert, California.

period (the results of 3 surveys in September were lost when our vehicle was burglarized) along a 500-km-long route consisting of paved and graded dirt roads. The route was categorized based on land use: (1) rangelands (primarily creosote scrub), (2) urban (small towns), and (3) irrigated agriculture (vineyards and citrus groves).

Surveys began at sunrise and required approximately 8 h to complete. Primary (interstate) roads along the route were driven at 85–110 km hr^{-1}, while secondary (2-lane paved) and unpaved roads were driven at 30–85 km hr^{-1}. Our speed was scaled by our ability to drive safely and to scan the terrain. We altered direction and starting point of transect coverage to ensure each area was surveyed during different times of the day (sensu Bunn et al. 1995). All individual Turkey Vultures (*Cathartes aura*), Red-tailed Hawks (*Buteo jamaicensis*), Golden Eagles (*Aquila chrysaetos*), American Kestrels (*Falco sparverius*), Prairie Falcons, Common Ravens, and Loggerhead Shrikes within 365 m of the road were noted and the following information recorded: time of day, behavior (standing on the ground, perched, flying, soaring), and, if perched, perch type (cliff, tree, telephone pole, transmission tower, building, sign, other). When bird identification was problematic, we stopped the vehicle. An index of potential perch sites, defined as any structure (natural or artificial) >3 m in height, was obtained by counting all available perch sites within 365 m on both sides of the survey route.

As an index of bird abundance, we computed the mean number of bird sightings/100 km for the 7 species observed, by month and by year. For species with >120 sightings (Turkey Vulture, Red-tailed Hawk, Loggerhead Shrike, Common Raven), we evaluated frequency of observation as a function of land use. The greatest part of our survey route ran through creosote scrub (482.4 km), which was used for grazing, while lesser amounts passed through urban areas (14.4 km) and irrigated agriculture (3.2 km). Within the primary land use along our survey route (rangeland), we compared numbers of birds/100 km with the number of linear rights-of-way that ran in parallel (sensu Knight et al. 1995). This number could be as high as 5 when one or more railroad tracks, transmission powerlines, highways, and telephone pole lines paralleled each other. For the entire survey route and for all species except Golden Eagles (with too few observations), the relative frequency of behavioral patterns for each species was calculated. Also, for these species we calculated the proportion of perch-site use using our potential perch site indices to compute expected values. Because our data were not normally distributed (UNIVARIATE procedure; SAS Institute Inc. 1990), we used the Kruskal-Wallis test (chi-square approximation; NPAR procedure; SAS Institute Inc. 1990) to examine relationships between bird numbers among months, bird numbers and land use, and bird numbers and number of linear rights-of-way in parallel. To test for differences in perch-site use and behavior, we used χ^2 goodness-of-fit tests (PROC FREQ; SAS Institute Inc. 1990).

RESULTS

Populations

Ravens were observed most frequently, with Turkey Vultures, Red-tailed Hawks, Loggerhead Shrikes, American Kestrels, Golden Eagles, and Prairie Falcons seen in decreasing numbers (Table 1). Ravens and Red-tailed Hawks were seen on every survey, while shrikes (81%), kestrels (69%), and Prairie Falcons (56%) were seen on over half the surveys. Turkey Vultures were seen on less than half the surveys (46%), and Golden Eagles were seen on only 3 surveys (6%).

For each species, other than Golden Eagles, there were significant among-month differences in numbers (Table 1; Kruskal-Wallis, all χ^2 values > 17, $n = 45$, df $= 11$, all P values < 0.03). Raven numbers were highest during winter and lowest during spring and early summer. Vultures were first seen on the study area in March and not seen after October. American Kestrels, Prairie Falcons, Red-tailed Hawks, and Loggerhead Shrikes were seen year-round and appeared to be most numerous during winter. Golden Eagles were the least common species, with only 4 seen.

Land Use and Linear Rights-of-Way

Turkey Vultures, Red-tailed Hawks, and ravens were most numerous on irrigated agricultural lands and least numerous on rangelands, while shrikes were most common at urban sites (Table 2; Kruskal-Wallis, all χ^2 values > 21, $n = 45$, df $= 2$, all P values < 0.0001). Raven numbers increased with increasing number of linear rights-of-way parallel to the survey route (Kruskal-Wallis, $\chi^2 = 38.08$, df $= 3$, $P = 0.0001$), although this pattern was not apparent for Turkey Vultures, Red-tailed Hawks, and Loggerhead Shrikes (Fig. 2).

Behavior and Perch-site Use

Perching was the most often observed behavior for all species other than ravens (Fig. 3). Between 42% and 87% of Turkey Vulture, Red-tailed Hawk, American Kestrel, Prairie Falcon, and Loggerhead Shrike observations were of perched birds, while ravens were most often observed flying or soaring. In addition, Turkey Vultures and ravens also were seen on the ground (18% and 28% of all observations, respectively; Fig. 3). Of all vultures and ravens seen on the ground, 42% and 39%, respectively, were seen on roads.

For all species, birds did not use perch sites proportionately to availability (all χ^2 values > 1000, df $= 5$, all P values < 0.001; Fig. 4). Transmission powerline towers and telephone poles were the most frequently used perch types for all species (Fig. 4). Ravens showed the greatest plasticity in use of perches, utilizing all perch types.

DISCUSSION

Populations

Raven numbers were highest during December and January, an observation also noted by Austin (1971). During winter ravens are not spatially tied to nesting sites and food is less common and more ephemeral. Accordingly, ravens are able to form flocks and utilize concentrated sources of food that are either dependable (e.g., landfill sites) or sporadic in occurrence (e.g., road-killed animals; Heinrich 1989).

Turkey Vultures were present from March through October and were most numerous during June. Turkey Vultures are migratory in the Mojave Desert (Small 1994), which our results corroborate. A similar pattern was found for Turkey Vultures in New Mexico (Eakle et al. 1996). Red-tailed Hawks, Prairie Falcons, and American Kestrels were observed more frequently during the winter months, perhaps reflecting an augmentation of northern-latitude birds during winter months as well as offspring following nesting. Eakle et al. (1996) also noted that Red-tailed Hawks are much

TABLE 1. Mean number/100 km ($\pm s_{\bar{x}}$) of predatory birds seen by month in the Mojave Desert, California, December 1992 to November 1993.

Species	Number of birds/100 km												
	Dec 1992	Jan 1993	Feb 1993	Mar 1993	Apr 1993	May 1993	Jun 1993	Jul 1993	Aug 1993	Sep 1993	Oct 1993	Nov 1993	Total
Turkey	—	—	—	0.30	0.78	0.97	4.93	1.35	1.52	0.90	3.11	—	1.72
Vulture	—	—	—	(0.06)	(0.08)	(0.36)	(1.44)	(0.39)	(0.62)	a	(0.00)	—	(0.31)
Red-tailed	1.63	1.74	1.07	0.81	0.78	0.95	0.63	1.85	1.21	1.79	1.01	1.79	1.21
Hawk	(0.11)	(0.32)	(0.11)	(0.27)	(0.27)	(0.19)	(0.16)	(0.38)	(0.26)	a	(0.30)	(0.24)	(0.09)
Golden	0.67	—	—	—	—	—	—	—	—	—	—	0.22	0.45
Eagle	(0.00)	—	—	—	—	—	—	—	—	—	—	(0.00)	(0.05)
American	0.56	0.75	0.56	0.60	0.22	—	0.50	0.34	0.36	0.22	0.22	0.22	0.46
Kestrel	(0.14)	(0.17)	(0.21)	(0.17)	(0.00)	—	(0.17)	(0.06)	(0.06)	a	(0.00)	(0.00)	(0.04)
Prairie	0.22	0.45	0.50	0.52	—	0.34	0.30	0.30	0.22	0.45	0.67	0.22	0.42
Falcon	(0.00)	(0.11)	(0.21)	(0.06)	—	(0.08)	(0.06)	(0.06)	(0.00)	a	(0.20)	(0.00)	(0.04)
Loggerhead	3.45	0.84	1.01	0.81	0.67	3.11	0.95	1.79	0.40	0.67	0.50	0.67	0.81
Shrike	(0.00)	(0.11)	(0.32)	(0.33)	(0.00)	(0.00)	(0.13)	(0.24)	(0.11)	a	(0.14)	(0.24)	(0.08)
Common	10.59	11.04	5.89	3.54	5.94	4.48	8.21	6.73	7.98	2.02	6.17	6.95	6.91
Raven	(0.69)	(1.35)	(0.54)	(0.50)	(0.89)	(0.43)	(2.34)	(0.63)	(2.62)	a	(1.75)	(0.71)	(0.51)

[a] Data from only 1 survey

TABLE 2. Mean number per 100 km (± *s*) of Turkey Vultures, Red-tailed Hawks, Loggerhead Shrikes, and Common Ravens seen at different land-use types, east Mojave Desert, California.

	Number of birds/100 km ± *s*			
Land use	Turkey Vulture	Red-tailed Hawk	Loggerhead Shrike	Common Raven
Rangeland	0.4 ± 0.6	1.2 ± 0.6	0.6 ± 0.6	3.7 ±1.9
Irrigated agriculture	7.8 ± 37.3	8.5 ± 21.1	0.7 ± 4.5	255.2 ± 363.0
Urban	3.6 ± 14.3	1.3 ± 2.7	1.9 ± 3.4	48.2 ± 41.2

more common during fall and winter in New Mexico. Finally, although Loggerhead Shrikes are migratory in other parts of their range, they were seen year-round in our study area (see Small 1994:207).

Golden Eagles were the species seen least commonly. These findings are surprising as Golden Eagles are a regular nesting bird in the Mojave Desert, albeit a species that occurs naturally at low densities due to its large area requirements. Our findings might reflect the naturally low density of eagles, or they may be a result of our survey route not traversing eagle nesting areas. Though speculative, the fact that our only observations were during winter suggests that eagles in the Mojave may undergo elevational migrations from the desert mountain ranges where they nest during summer to desert basins where they occur during winter (Small 1994).

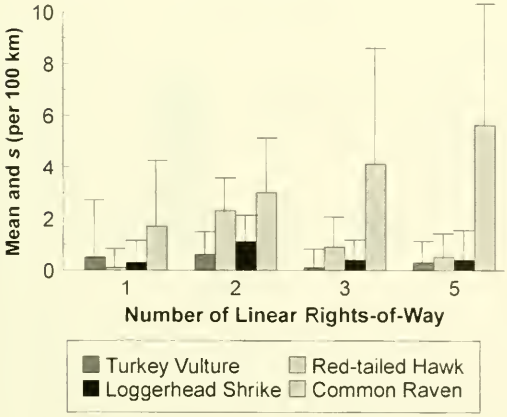

Fig. 2. Mean number per 100 km (± *s*) of Turkey Vultures, Red-tailed Hawks, Loggerhead Shrikes, and Common Ravens seen adjacent to number of linear rights-of-way, east Mojave Desert, California.

Land Use and Linear Rights-of-Way

Turkey Vultures, Red-tailed Hawks, and ravens were most numerous on irrigated agricultural lands and urban areas and less common on rangelands. We suggest these elevated numbers reflect increased abundance, availability, and dependability of food sources (Knight et al. 1993). Urban and agricultural areas are associated with high road traffic and road densities, providing increased levels of road-killed carrion (Knight and Kawashima 1993). In addition, these 2 land uses provide plentiful year-round water and abundant potential nesting sites (e.g., buildings, signs, ornamental trees). For example, almost half (46%) of all raven sightings were made at 2 localities, a small town and a citrus/vineyard complex, which together comprised only 1% of the survey route. The Cadiz Land Company vineyard provides abundant year-round water and a variety of food (i.e., citrus, grapes) in season. The small community of Ludlow appears to be of importance to ravens as it has a sanitary landfill that provides a predictable food supply.

Given that ravens show elevated numbers along linear rights-of-way (Knight and Kawashima 1993), it is not surprising that we found a positive relationship between raven numbers and increasing number of rights-of-way. This finding supports a similar relationship reported for ravens during summer months in the Mojave (Knight et al. 1995).

Behavior and Perch-site Use

Red-tailed Hawks, American Kestrels, Prairie Falcons, and Loggerhead Shrikes were most often seen perching, a frequently used mode of hunting for these species (Bent 1950, Brown and Amadon 1968). Although transmission powerline towers and telephone poles were among the least common potential perch

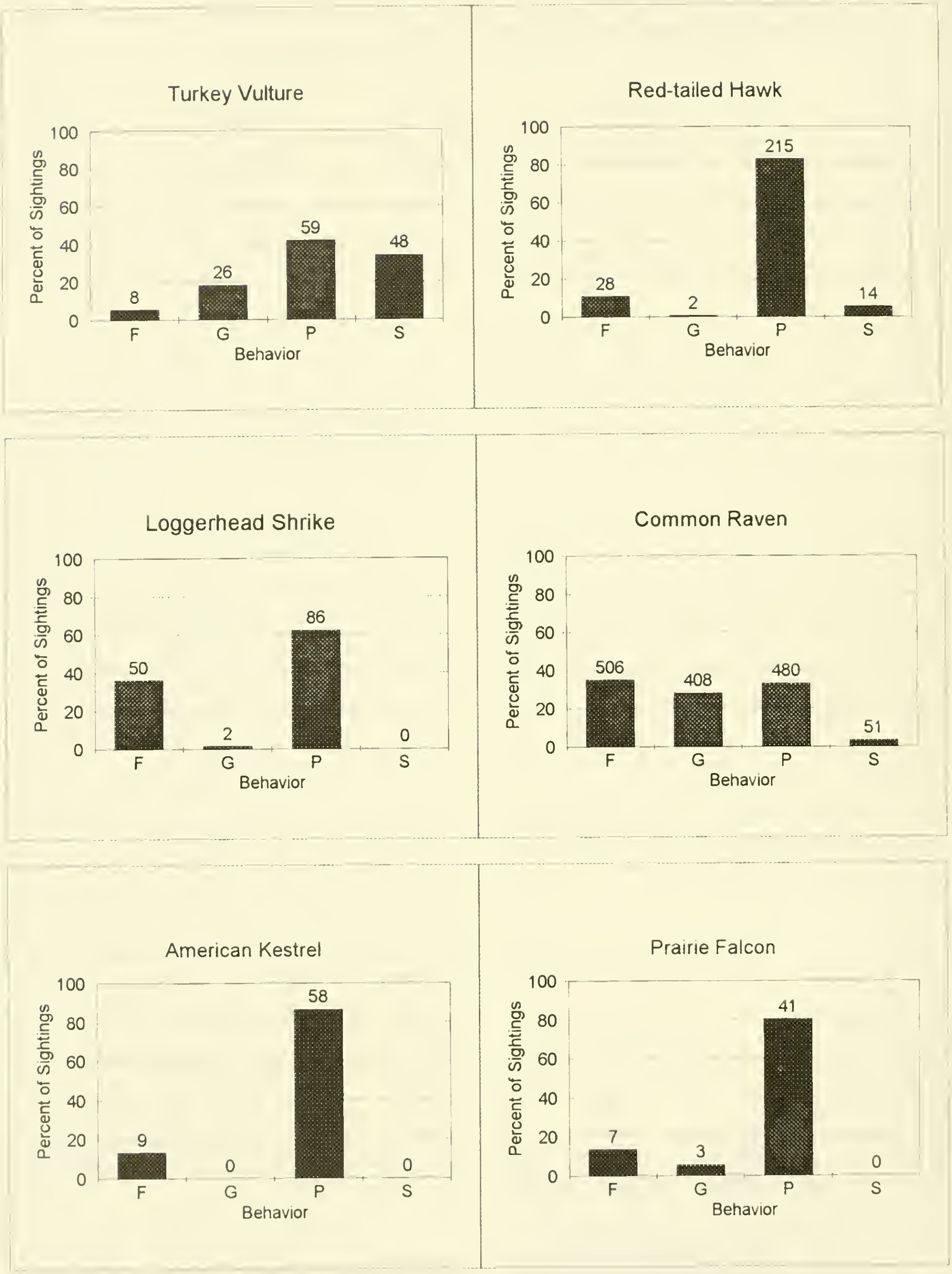

Fig. 3. Proportion of 6 species of predatory birds seen flying (F), standing on the ground (G), perched (P), or soaring (S), east Mojave Desert, California.

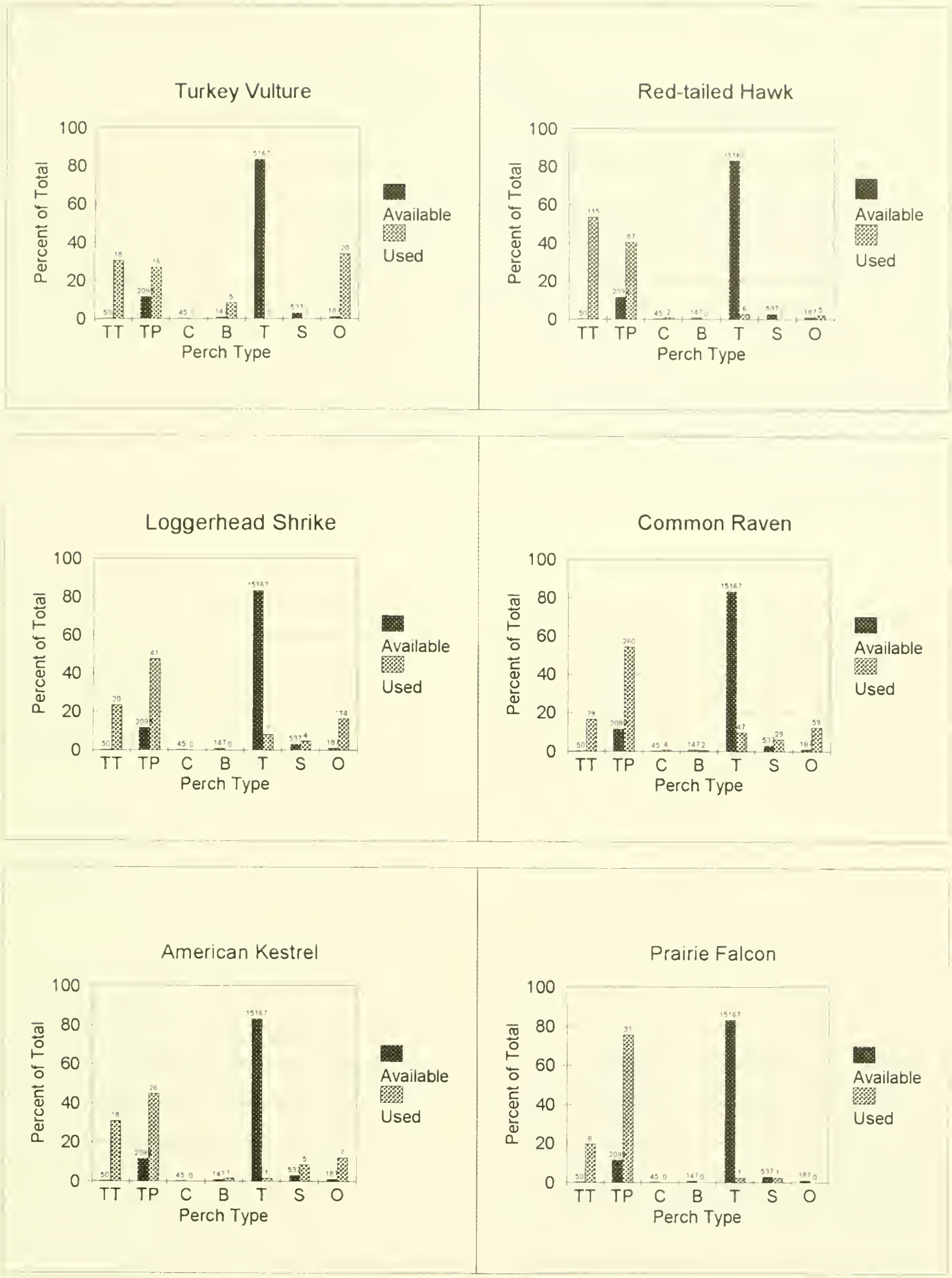

Fig. 4. Proportion of perch types used by 6 species of predatory birds, east Mojave Desert, California. TT – transmission tower, TP – telephone pole, C – cliff, B – building, T – tree, S – sign, O – other.

sites, they were the most frequently used structures by all species. Ravens and Turkey Vultures were often seen on the ground, particularly along roads, reflecting their propensity to scavenge road-killed wildlife (Knight and Kawashima 1993). Stahlecker (1975) found that although transmission towers constituted only 1.5% of available perches in a grassland area in Colorado, 81% of raptors seen during surveys utilized them as perches. Likewise, Craig (1978) noted that almost 78% of all raptors observed perched along a 187-km survey route in Idaho were on power poles or wires. In the Mojave Desert tall powerline towers and telephone poles, when compared with shorter perch sites such as trees or signs, may provide birds with a wider range of vision, easier takeoff, and greater attack speed when hunting prey on the ground (Knight and Kawashima 1993).

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ENVIRONMENTAL EFFECTS ON COMMON SNIPE WINNOWING AND CALLING (ACTIVITY)

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Abstract.—Our objective was to clarify the effects of 10 identified variables on snipe activity (winnowing and calling) by demonstrating correlations between the variables and snipe activity. We monitored snipe at 2 study areas in southwestern Montana and northwestern Wyoming at all hours of the day and night during the 1996 and 1997 breeding seasons. We measured 10 variables at established points along transects that were situated through the middle of each study site (8 study sites total). A total of 1200 monitoring periods were conducted throughout the course of this study. Effects of each factor on snipe activity were considered by examining general trends in each factor's graphical representation. Our results identified 6 factors (season, time of day, lunar cycle, solar radiation, wind speed, and temperature) that are associated with snipe activity. Snipe were most active early in the breeding season during 2 twilight periods during the first and last quarters of the lunar cycle. Low solar radiation levels, wind speeds, and temperatures were also most ideal conditions for snipe activity. All 6 factors should be considered when attempting to detect, survey, or estimate snipe populations.

Key words: snipe, Gallinago gallinago delicata, *monitoring, temporal factors, meteorological factors, abundance, trends, surveys.*

Common Snipe (*Gallinago gallinago delicata*; AOU 1983, Tuck 1955) behavior patterns on breeding grounds are poorly understood. The snipe's mobility, elusiveness, and mythological characteristics such as capturing the bird with a bag and stick contribute to this lack of knowledge. After reviewing the literature on snipe, we identified 10 factors that might influence snipe winnowing and calling. Winnowing is an aerial flight pattern performed over a large area. Both male and female snipe winnow, but it is primarily done by males. Birds fly high into the air and drop rapidly toward the ground. Tail feathers are spread apart and air vibrates the feathers, producing a sound (winnowing). Calling is a form of vocalization usually produced by birds on the ground. Most observations of winnowing and calling are from 2 authors (Robbins 1952, 1954, Tuck 1955, 1972), but data regarding effects of variables on snipe winnowing and calling are conflicting. Quantifying the effects of environmental factors and using this knowledge (peak activity times, conspicuousness, etc.) can be helpful in planning fieldwork and selecting productive survey methods (Robbins 1981). However, this rarely has been done (Best 1981).

Consequently, our objective was to clarify the effects of 10 variables (season, time of day, lunar cycle, cloud cover, precipitation, wind speed, temperature, solar radiation, fog, and disturbances, which include cool temperatures, low wind, and clear sky) on snipe activity (winnowing and calling) by demonstrating general correlations between the factors and activity.

Study Areas

We studied Common Snipe at Red Rock Lakes National Wildlife Refuge (RRLNWR), Montana, in 1996 and along the Green River north and west of Pinedale, Wyoming, in 1997 (Fig. 1). Pinedale and RRLNWR are considered study areas and habitat units. Low, bog, red, green, tosi, schwabachers, wagstaffs, and duck are study sites at the 2 areas. RRLNWR is located in southwestern Montana in Centennial Valley approximately 80 km west of Yellowstone National Park. The Gravelly and Centennial Mountain ranges border the refuge to the north and south, respectively (Fig. 1). Habitats range from high-elevation marsh at 2000 m to alpine at 3000 m above sea level.

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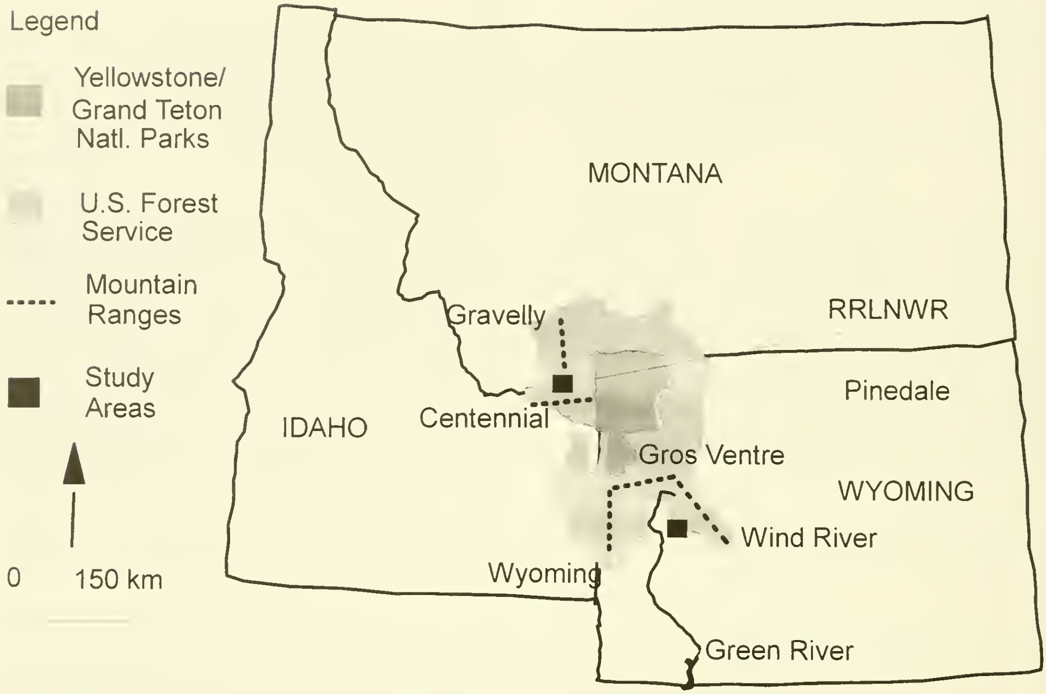

Fig. 1. Location of Red Rock Lakes National Wildlife Refuge and Pinedale study areas in Montana and Wyoming.

Two large lakes lie in the center of the 17,604-ha refuge and are fed by 17 creeks. Common Snipe are associated with fens, marshes, and sloughs located throughout the refuge. In particular, they prefer shallow-water areas averaging 30–40 mm in depth that are dominated by beaked sedge (*Carex rostrata*) and some shrub cover such as willow (*Salix* sp.), bog birch (*Betula glandulosa*), or shrubby cinquefoil (*Potentilla floribunda*; Nelson 1979).

RRLNWR headquarters is located in Lakeview, Montana, approximately 40 km east of I-15 exit 1 (Monida Pass) on a dirt road that follows the Montana-Idaho border. Montana study sites are described in relation to Lakeview. The low lake site (0.53 km^2) is approximately 2 km west of Lakeview along Red Rock Road and south of Lower Lake where a stand of willows is located in a sea of sedges and rush. The bog site (0.85 km^2) is located 12 km east of Lakeview on Red Rock road just south of Upper Lake. Red Rock Creek site (0.64 km^2), 21 km east of Lakeview along Red Rock road, is a willow riparian habitat on the north side of the road; it follows Red Rock Creek east to the refuge boundary.

Pinedale, in northwestern Wyoming, is approximately 215 km south of Yellowstone National Park along state highway 191. The town is surrounded by the Wyoming, Gros Ventre, and Wind River Mountain ranges to the west, north, and east, respectively (Fig. 1). Habitats range from grassy meadows and sagebrush (*Artemisia* sp.) for cattle grazing at 2200 m to alpine tundra and glaciers at 4200 m. Because the Green River is a major drainage for the Wind River Mountains, spring water coverage and depth vary with the amount of winter snow. Common Snipe use willow riparian areas and subirrigated meadows along the Green River, where dominant herbaceous plants consist of beaked sedge, water sedge (*Carex aquatilis*), and timothy (*Phleum* sp.).

Duck Creek site (1.63 km^2) is approximately 8 km west of Pinedale along state highway 191. Located on the north side of the road, it is a section of state land that allows fishing access to Duck Creek and has a parking area off the highway. Schwabacher ranch site (1.94 km^2) is approximately 12 km west of Pinedale on Quarter Circle 5 Ranch owned by Jackson Schwabacher. The site is on the south side of the highway along Faler Creek. Wagstaff Ranch site (1.88 km^2) is on county road 354, locally called Horse Creek Road. County road 354 is located at Daniel Junction 16 km west of Pinedale on state highway 191. Green River (1.56 km^2) and Tosi Creek sites (0.94 km^2) are approximately 40 km north of state highway 191 on county road 352. Green River site is approximately 16 km north of the Kendall guard station on the west side of the Green River, and Tosi Creek site is approximately 25 km northwest of Kendall just south of Moore Ranch (site butts up against the ranch boundary). Both sites are located off a forest service road that heads to Mosquito Lake.

METHODS

In 1996 we monitored snipe at 3 study sites (low, red, and bog) on RRLNWR between 0500 h and 1900 h MST. Each study site was located along the lake in willow sites 800–1000 ha in size. A straight-line transect was established through the middle of each study site with 10 sample points spaced 500 m apart. Points were spaced 500 m apart and on each side of the transect so we could adequately sample the relatively small area. Before nesting occurred (15 April–23 May), we measured 10 variables at each established point. While collecting these data, we also monitored snipe activity by counting the number of snipe heard. We determined that birds could be heard for approximately 500 m. Following nesting (24 May–15 July), we measured the 10 variables while monitoring previously radio-transmittered snipe (n = 10). Nine of 10 transmittered snipe were located at the bog study site and were monitored twice daily (morning and afternoon). We then used data from marked and unmarked birds. To standardize snipe monitoring efforts, a 10-min time period was established. We also divided the 10 variables into categories (Table 1).

In 1997 we monitored snipe at 5 study sites near Pinedale, Wyoming. These sites were approximately 500 ha in size and located in willow communities. Transects were established through the middle of each site with points spaced 1 km apart. From 17 April to 30 June, we monitored snipe activity from points on the transect while measuring the 10 variables. We did not use radio telemetry in 1997. Also, monitoring in July 1997 was eliminated because snipe were inactive. In 1996 we rarely (<5% of the time) counted additional snipe during the last 4 min of monitoring; thus, in 1997 we decreased our listening time from 10 to 6 min. This did not affect the number of snipe heard/counted.

RESULTS

We conducted a total of 1200 monitoring periods, 6 or 10 min each, throughout the course of this study. Initially, the effects of each factor on snipe activity were considered by examining general trends apparent in each factor's graphical representation. Two variables (fog and disturbances) could not be evaluated as no data were available.

Temporal Variables

SEASON.—Snipe activity was most pronounced in May (Fig. 2). The peak in activity occurred early in the breeding season followed by a steady decline.

TIME OF DAY.—Snipe were slightly active throughout the day and night, but were most active during dusk (post-sunset) and late-night (predawn) periods (Figs. 2, 3).

Meteorological Variables

LUNAR CYCLE.—During the first and last quarters, we heard more snipe than we did when a full moon or no moon was present (Fig. 2). A few snipe were active throughout the night regardless of moon phase, but more activity occurred at dusk, especially during the first quarter.

CLOUDS.—We heard more snipe on very cloudy or overcast days. We heard fewer snipe on other days, although numbers were basically equivalent whether the days were clear or partly cloudy (Fig. 3).

PRECIPITATION.— We recorded more snipe activity during rain than during drizzle or no precipitation (Fig. 3). Rain did not seem to affect snipe activity adversely; in fact, we recorded a considerable amount of activity during some inclement weather. However, hail (2–10 mm in size) caused snipe to stop winnowing immediately. Rain probably affected our ability to hear more than it did snipe activity.

WIND SPEED.—We heard more activity when wind speed was <8 km/h (Fig. 4). Activity decreased with wind speeds of 8–13 km/h

TABLE 1. Ten variables that can affect snipe activity, with accompanying categories and collection methods.

Variable	Categories	Collection methods
Season	April, May, June, July	Calendar
Time of day (MST)	Morning (0500–1030 h) Late morning (1031–1330 h) Early afternoon (1331–1630 h) Late afternoon (1631–1900 h) Dusk (1901–2200 h) Early night (2201–2400 h) Midnight (0001–0300 h) Late night (0301–0500 h)	Watch
Lunar cycle	First quarter Last quarter Full moon No moon or less than a quarter	Calendar and field observation
Cloud cover	No clouds (0%) Partly cloudy (1–50%) Very cloudy (51–100%) Overcast (100%)	Field observation
Precipitation	None Rain Light snow (could see) Heavy snow (couldn't see)	Field observation
Wind speed (km/h)	0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10+	Dwyer® handheld wind meter[a]
Temperature (°C)	minus 13–0, 1–5, 6–10,11–15, 16–20, 21–23	Campbell Scientific Datalogger[b]
Solar radiation (W · m^2)	0–1, 2–100, 101–200, 201–300, 301–400, 401–500, 501–600, 601–700, 701–1200	Campbell Scientific Datalogger[b]
Fog	Distance observer could see	Field observation
Disturbances	Any loud noise such as train whistles, backfires from car, or low-flying airplanes	Field observation

[a] Instrument purchased from Forestry Suppliers Inc., Jackson, MS.

[b] Instrument purchased from Campbell Scientific, Inc., Logan, UT.

(Fig. 4). At greater velocities we could not determine whether activity diminished or our ability to hear it was impaired.

TEMPERATURE.—Common Snipe were moderately active at temperatures of 6–10°C (Fig. 4). Snipe appeared to be most active when the temperature was below 6°C.

SOLAR RADIATION.—Snipe activity was greatest during the lowest level of solar radiation (0–1 Watt • m^2; Fig. 4). This threshold seemed very important to snipe.

DISCUSSION

From our evaluation of 10 variables identified from the literature, we subsequently identified 6 (season, time of day, lunar cycle, solar radiation, wind speed, and temperature) that appeared to influence snipe activity (Figs. 2, 4).

Season

Snipe are most active early during the breeding season (Tuck 1972, Smith 1981, Taylor 1978). We found snipe activity to be highest in May. This peak in activity is influenced by the arrival of females (Tuck 1972), latitude, and weather conditions (Tuck 1972). During this time snipe compete for mates, secure pair bonds, and defend territories.

Time of Day

Snipe activity varies by time of day, as with most birds. We found snipe to be most active during the 2 twilight periods. Similar results

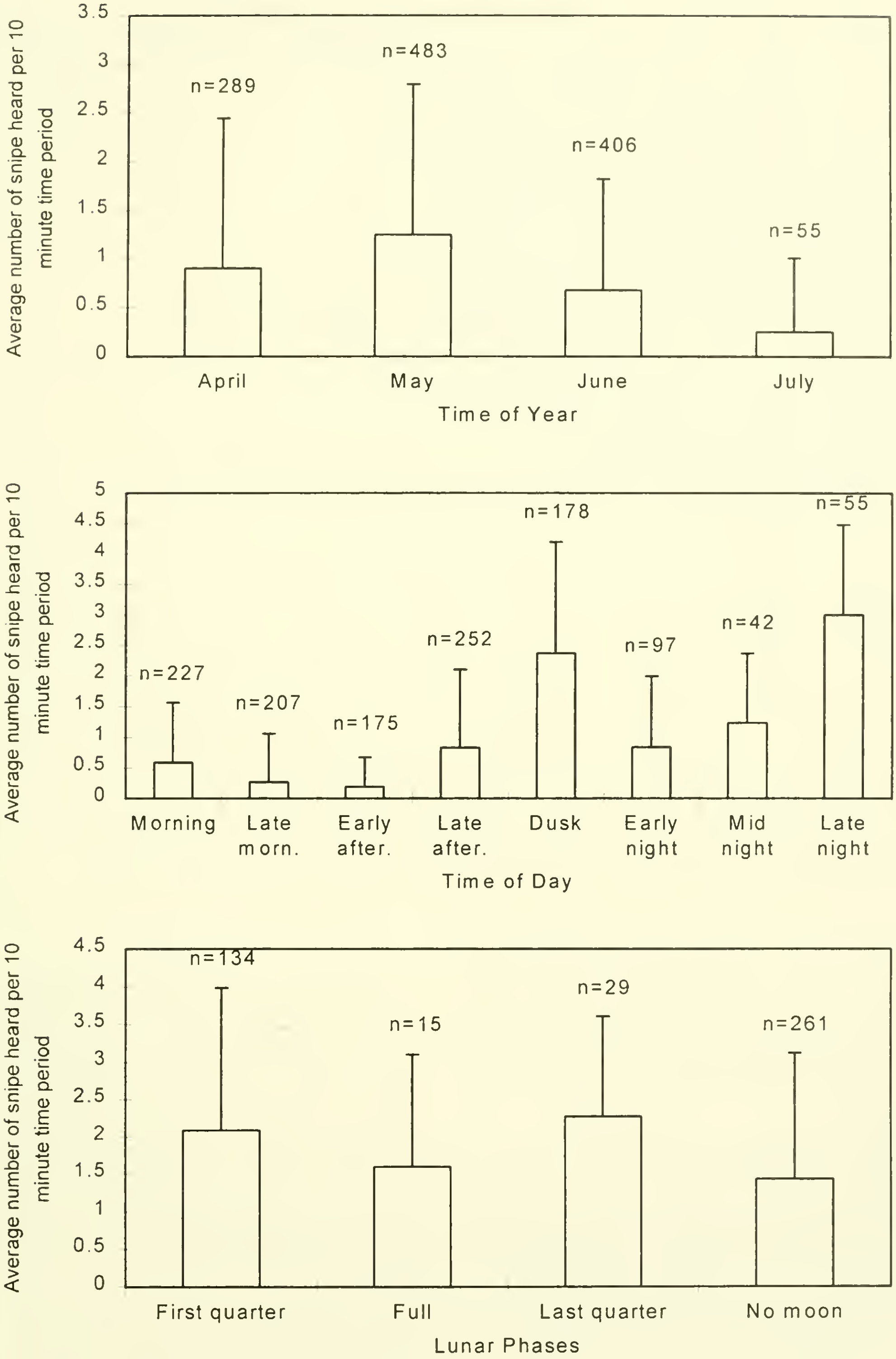

Fig. 2. Effects of season, time of day, and lunar phases on average number of snipe heard during 1996–97 breeding seasons at Red Rock Lakes National Wildlife Refuge and Pinedale study areas. Error bars represent 1 standard deviation. Data are based on 10-min counts in 1996 and 6-min counts in 1997.

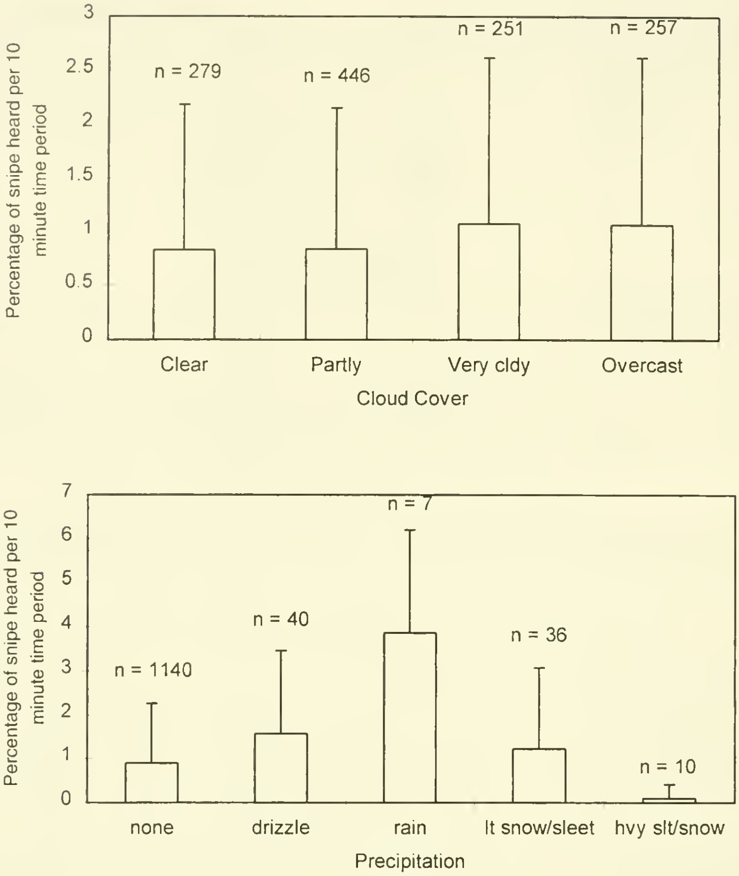

Fig. 3. Effects of cloud cover and precipitation on number of snipe heard during 1996–97 breeding seasons at Red Rock Lakes National Wildlife Refuge and Pinedale study areas. Error bars represent 1 standard deviation.

were found by Robbins (1952), Tuck (1972), and McKibben and Hofmann (1981). However, we agree with the majority of authors (Burleigh 1951, Solman 1954, Tuck 1972, McKibben and Hofmann 1981) that snipe are most active in the post-sunset or dusk twilight period.

We realize that our data (Fig. 2) illustrate otherwise and attribute the higher average during the late-night period to our monitoring protocol. Most observations for the late-night period were made early in the breeding season when snipe are more active regardless of time of day. During the dusk time period, our observations were conducted equally throughout the breeding season. Precipitation (Fig. 3) could also be misleading, as most rain and snow occurred early in the breeding season.

Lunar Cycle

We heard more snipe during the first and last quarters than when a full moon or no moon (less than a quarter or absent, new moon) was present (Fig. 2). Contrary to our results, however, effects of a bright moon have been reported in the literature to increase the winnowing period and/or cause snipe to winnow throughout the night (Robbins 1952, Tuck 1955).

Snipe migrate at night during moonlight periods (Tuck 1972) and keep in contact with each other by producing scaipe notes, which are barely audible to the ground observer (Tuck 1972). Zugunruhe (migratory restlessness) is demonstrated by snipe in late February or early March in Florida (Fogarty 1970). At this time snipe flush and wheel around in flocks and drop abruptly to the ground (Fogarty 1970).

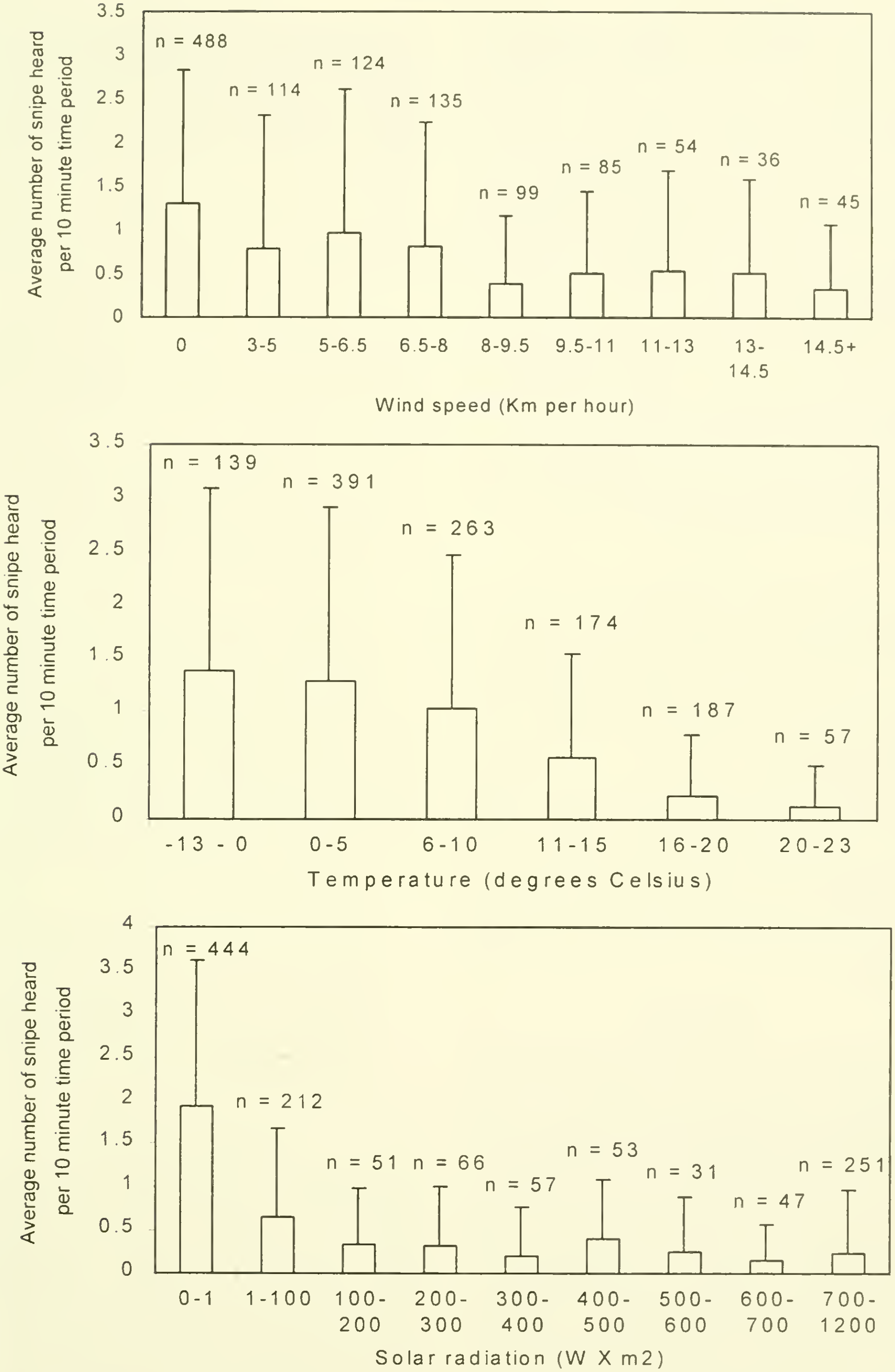

Fig. 4. Effects of wind speed, temperature, and solar radiation on average number of snipe heard during 1996–97 breeding seasons at Red Rock Lakes National Wildlife Refuge and Pinedale study areas. Error bars represent 1 standard deviation.

Spring migration begins on the first moonlight night after zugunruhe (Fogarty 1970, Fogarty and Arnold 1977, Arnold 1994). Fall migration is affected by phases of the moon as well as location and intensity of high- and low-pressure fronts (Tuck 1972). Long-distance migration occurs only on moonlight nights (Tuck 1972). The first fall flights occur during the last quarter in August, with peak flights occurring during the full moon in September and first quarter in October (Tuck 1972).

We suggest that, based on the data presented above, snipe use the moon to determine seasonal time. In addition, the last quarter of the moon phase is present only during the late-night time period. For these reasons we believe the lunar cycle has definite effects on snipe activity (winnowing and calling) and behavior (breeding, migration).

Solar Radiation

Snipe were most active during the lowest solar radiation level (0–1 W • m^2; Fig. 4). Measurements of solar radiation have been attempted only recently (past 20 yr approximately) due to technological advances. However, the inability to measure solar radiation beforehand did not discourage past researchers from noting its effects on snipe activity. Irregularity in winnowing periods could be caused by variations in light intensity (Tuck 1972, Taylor 1978). The change from maximum light to darkness in a short period of time could stabilize activity during the post-sunset period (Tuck 1955).

Wind Speed

Wind speeds >8 km/h decreased snipe activity. More activity was recorded when wind speeds were <8 km/h (Fig. 4). Effects of wind on snipe have been documented frequently (Robbins 1954, Tuck 1972, Taylor 1978). Robbins (1954), who found results similar to ours, suggested that wind may be the single most important factor influencing winnowing. Considering that winnowing is a high-speed dive that vibrates outer tail feathers, one can easily see how high wind speeds could affect this activity. Although most authors have not quantified their observations of wind on snipe activity, their previous research nevertheless supports our now-quantified data.

Temperature

Snipe activity was greatest below the 6–10°C range (Fig. 4). Snipe prefer cooler temperatures, a fact which has been documented previously (Robbins 1954, Tuck 1972, Taylor 1978). Robbins (1954) reported higher counts on cool mornings and very low counts when the temperature reached 10°C. On hot days winnowing is delayed approximately 0.5 h (Tuck 1972).

SUGGESTIONS FOR FUTURE STUDY

Although we could not measure the following variables due to time constraints, they should be considered when monitoring snipe:

- Cloud cover (clouds may decrease bird predators, allowing snipe to be more active; also, clouds are related to solar radiation levels)
- Density (activity may be density dependent)
- Territory size (this may be related to density, particularly how varying numbers of snipe relate to differing area sizes)
- Competition (related to density and territory size; both can influence numbers of snipe present, which may affect competition for mates)
- Habitat types (related to density and territory size; different types support varying numbers of snipe)
- Number winnowing at once (many snipe winnowing with varying intensities can confuse an untrained ear)
- Social structure (relationships between breeders and nonbreeders/floaters can influence interpretation of surveys; Baskett et al. 1984).

ACKNOWLEDGMENTS

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CHARACTERISTICS OF WHITE-TAILED DEER FAWN BEDS, BLACK HILLS, SOUTH DAKOTA

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Abstract.—Forty-two white-tailed deer fawns (*Odocoileus virginianus dakotensis*) were captured and fitted with radio transmitters and observed from June through September 1991 and 1992 to determine diurnal bed site use in the Black Hills of South Dakota. Fawns were monitored biweekly during daylight hours and 259 bed sites were located. In addition, 301 random sites were measured for comparison. Of 31 habitat variables measured, 8 were significant to determine use by fawns for a bed site when compared with random sites. Sites used by fawns were in relatively open stands of ponderosa pine (*Pinus ponderosa*) with mean basal area of approximately 11 m^2/ha compared to 16 m^2/ha in random sites. Fawn bed sites had greater mean vegetation cover, which ranged from 28.1% to 36.0%, compared with 19.9% and 33.8% at random sites in 1991 and 1992, respectively. Mean vegetation height was 101 cm at bed sites compared to 75 cm at random sites. Current timber harvest standards for stocking levels of pine range from 14 m^2/ha to 18 m^2/ha in the Black Hills, which are similar to our random sites. These levels preclude adequate development of understory characteristics used by white-tailed deer fawns for bed sites.

Key words: white-tailed deer, Odocoileus virginianus dakotensis, *fawns, bed sites, habitat, herbaceous cover, ponderosa pine, Black Hills.*

Winter often is considered the most critical time for many cervid populations in northern North America, and most earlier habitat research has emphasized winter range. White-tailed deer (*Odocoileus virginianus dakotensis*) in the Black Hills are no exception; conditions on winter range are critical to these migratory populations (Seig and Severson 1996). There is, however, a growing awareness that conditions on northern summer ranges may be equally important, particularly those relating to types and quality of habitat available to lactating females and their fawns.

Spring and summer habitat use patterns of adult females have been examined in the Black Hills (Kennedy 1992, Stefanich 1995, Deperno 1998), but fawn bed site use has not been studied. A fawn's choice of bed site is limited to the general area (macrohabitat) chosen by the doe. Although specifics for white-tailed deer are sparse, studies on other ungulates suggest the actual bed site is selected by the fawn (Marchinton and Hirth 1984, Huegel et al. 1986). Bed site location is critical to fawn survival because as neonates fawns spend most of their time lying down, often at a considerable distance from dams (Schwede et al. 1994). Cover at bed sites functions to hide deer from predators and to provide thermal cover (Huegel et al. 1986, Hyde et al. 1987).

The objective of this study was to examine habitat characteristics of white-tailed deer fawn bed sites to develop effective habitat management guidelines. The null hypothesis tested was that there are no differences in selected vegetative and physical attributes between fawn bed sites and randomly selected sites.

Study Area

The study was conducted in the northeastern Black Hills, South Dakota. The area includes about 39,000 ha, most of which is administered by U.S. Forest Service, Black Hills National Forest, although private lands are interspersed throughout. It is bounded by Interstate 90 on the east, U.S. Highway 14A on the north, U.S. Highway 385 on the west, and Nemo Road on the south.

Elevations range from 1068 m to 1677 m. Average annual precipitation ranges from 422 mm at Rapid City, just southeast of the study area, to 737 mm at Deadwood on the northwest.

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Average monthly temperatures during the coldest and warmest months (February and August) are −7.7° and 21.9°C at Rapid City and −8.8° and 16.1°C at Deadwood (NOAA 1994).

The study area is dominated by ponderosa pine (*Pinus ponderosa*) forest. The prevailing habitat type is ponderosa pine / snowberry / bearberry (*Pinus ponderosa / Symphoricarpos albus / Arctostaphylos uva-ursi*), as described by Thilenius (1972). White spruce (*Picea glauca*) with scattered stands of aspen (*Populus tremuloides*) occur sparingly on lower portions of north-facing slopes. Aspens also are found as stringers within upper drainages and often form a border between the ponderosa pine forest and riparian meadows. These meadows, dominated by Kentucky bluegrass (*Poa pratensis*) and mostly privately owned, were grazed by cattle and horses and/or hayed. National forest lands were grazed by cattle. Harvest of ponderosa pine, primarily by seed tree cuts or overstory removal, has been conducted throughout the study area.

METHODS

Capturing and Monitoring Fawns

White-tailed deer fawns were located via ground searches using doe behavior as an indicator of fawn presence (Huegel et al. 1985). Initial fawn searches encompassed the entire study area. Captured fawns were fitted with radio transmitters attached to expandable break-away collars. Total weight of transmitter and collar was 165 g. Collars were colored brown to match fawn pelage, and for 2 wk prior to placement they were stored in plastic bags containing fresh vegetation and/or pine needles. Handlers wore vinyl gloves during capture and collaring activities.

A total of 28 male and 14 female fawns were captured and fitted with radio transmitters over the 2-yr period. We monitored individual fawns during daylight hours every other week. Observations of 22 fawns began on 9 June 1991, and of 20 fawns 15 June 1992, ending 28 September 1991 and 21 September 1992. Vegetation was measured on a biweekly basis corresponding to fawn bed site location. Once bed sites were located, we marked the area and took vegetation measurements the following day.

Microhabitat Measurements

Microhabitat measurements were taken at all fawn bed sites and at random sites within the study area. Random sites were selected by computer-generated random numbers (Universal Transverse Mercator coordinates) within each section of the study area.

Using a 10-factor prism, we estimated tree basal area (BA) at each bed and random site center (Sharpe et al. 1976). Canopy cover of shrubs, grasses, and forbs, all by species, was estimated in twenty-four 0.1-m^2 quadrats (Daubenmire 1959) spaced at 1-m intervals along 2 perpendicular transects crossing at bed or random site center. Percent of area covered by slash, litter, rock, and bare ground was estimated in the same plots. We used a modified Robel pole with 2-cm alternating orange and white bands to estimate height density (based on visual obstruction, VOR) of understory vegetation (Robel et al. 1970). The pole was placed at bed/random site center and at 4 evenly spaced locations (90°) 2 m from center. Readings were taken at 4 evenly spaced locations (90°) around each pole for a total of 20 observations at each site. The 4 observations around the pole were read from a distance of 4 m at a height of 1 m. Following the same procedure, we used a 250-cm pole to estimate vegetation height. Overstory canopy cover was estimated using a spherical densiometer at site center and at the end of each transect for a total of 5 observations.

Statistical Analysis

We reduced data collected from each fawn bed and random site to 1 mean per attribute per site, for a total of 31 habitat variables. Data were examined for heterogeneous variances using Bartlett's test. When heterogeneous variances were detected, data were $\log_{10}$ transformed. Averages of bed and random sites were compared using multivariate testing of hypothesis based on centered bootstrap adjusted *P*-values (Wright 1992). Data could have been analyzed for each variable separately, but our concern was correlations among variables for the same observation. More specifically, the *P*-value produced in separate tests could be correlated, likely causing an incorrect declaration of significance in some cases. The multitest adjusts *P*-values to account for multiple correlation. We examined the variables year (1991, 1992), biweekly intervals (1–8), type (fawn, random), and interactions to test the hypothesis that fawn bed sites do not differ from random sites. Statistical inferences were made at a probability level of 0.10 for type I error to decrease type II error.

RESULTS AND DISCUSSION

A total of 42 fawns were captured, 22 in 1991 and 20 in 1992. Biweekly tracking of fawns resulted in the measurement of 259 diurnal bed sites, 127 of which we measured in 1991 and 132 in 1992. The number found per biweekly interval ranged from 12 to 20 in 1991 and 7 to 20 in 1992. Death losses were 23% and 35% for 1991 and 1992, respectively. As the season progressed, the number of fawns found biweekly declined because of mortality. Locations of bed sites were balanced among fawns that survived. Measurements also were collected on 301 randomly selected sites, 147 in 1991 and 154 in 1992. During each biweekly interval we measured 17–20 sites in 1991 and 14–22 in 1992.

We tested 31 habitat variables. Heterogeneity of variances could not be tested on 15 because of a preponderance of zero data. Since sample means were also small, we considered these variables relatively unimportant as components of fawn habitat and eliminated them from further consideration. Among these were percentage cover of rock (≤1%), bare ground (≤1%), and 10 shrub species (each <1%). Included were variables with low basal area for birch (*Betula papyrifera*), 1.3 m^2/ha; bur oak (*Quercus macrocarpa*), 0.3 m^2/ha; white spruce, ≤0.1 m^2/ha; and ironwood (*Ostrya virginiana*), 0.3 m^2/ha. No differences between bed and random sites were detected for 8 of the remaining 16 habitat variables; differences were found for the other 8 ($P \leq 0.10$). The 8 nonsignificant variables were vegetation height 2 m out from bed site, VOR at bed site and 2 m out from bed site, total understory canopy cover, total forb cover, Engelmann spruce (*Picea engelmannii*) basal area, canopy cover of bearberry and of Oregon grape (*Mahonia repens*).

Fawns used bed sites with greater mean grass cover ($P \leq 0.001$) in 1991; but no difference ($P = 0.112$) was noted in 1992 (Figs. 1a, b). While dense, herbaceous vegetation seems important for fawn hiding cover, there was less need for specific site selection in 1992 because there was more mean grass cover than during the previous year. Mean grass cover in 1991, for example, was only 19.9 ± 0.5% (mean ± $s_{\bar{x}}$) on random sites, while in 1992 it was 33.8 ± 1.6%. Fawns selected sites with 28.1 ± 1.6% and 36.0 ± 0.8% total grass cover during each respective year.

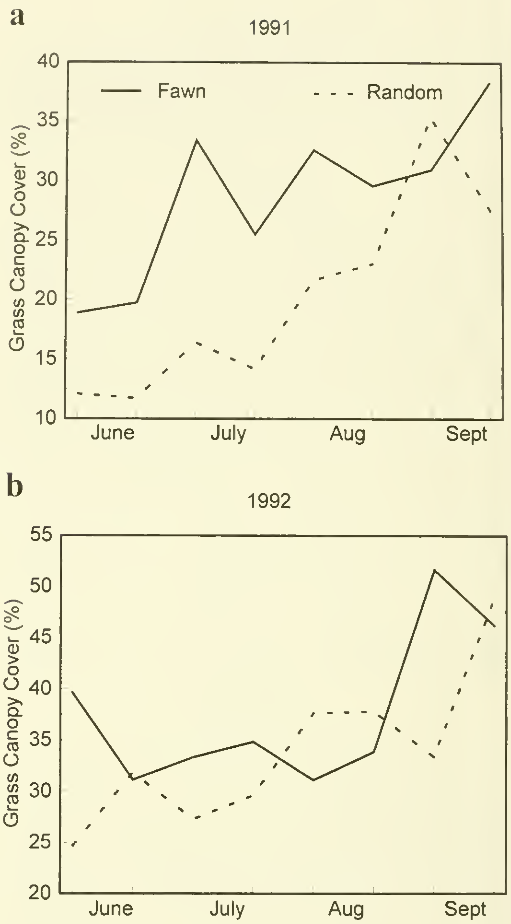

Fig. 1. Total canopy cover of grass (%) at white-tailed deer fawn bedding sites versus random sites at biweekly intervals from early June to late September 1991 (a) and 1992 (b), Black Hills, South Dakota. Significant at $P = 0.10$.

White-tailed deer fawns also used taller vegetation for bed sites than that found on random sites ($P \leq 0.001$). Mean vegetation height was 100.5 ± 8.3 cm on sites used by fawns and 75.4 ± 13.2 cm at random sites (Fig. 2). No differences were noted between years ($P = 0.897$).

Forbs were a relatively minor component of the flora. Mean forb cover was 17.7 ± 0.6% compared to 29.4 ± 0.9% and 27.0 ± 0.6% for grasses and shrubs for both years combined,

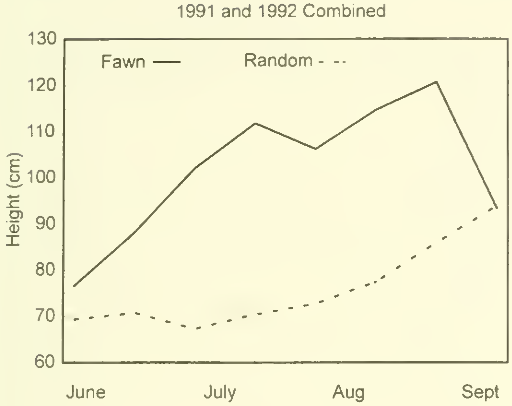

Fig. 2. Height of vegetation at bed sites used by white-tailed deer fawns versus random sites from early June to late September 1991 and 1992 combined. Black Hills, South Dakota. Significant at $P = 0.10$.

respectively. Even when many species of forbs are present, they often contribute less to total understory cover than grasses or shrubs, especially under pine canopy (Uresk and Severson 1989).

Although mean density (VOR) of vegetation tended to be greater at fawn bed sites in 1991 and 1992, differences were not significant ($P = 0.586$ and 0.924, respectively). Bed sites had a vegetation density of 16.3 ± 1.6 cm in 1991, while random sites had 12.6 ± 1.4 cm. Densities on bed and random sites in 1992 were 21.4 ± 2.5 and 17.7 ± 1.9 cm, respectively. Our results on VOR measurements differ from those of Hyde et al. (1987) and Huegel et al. (1986), who concluded that density of vegetation, based on VOR, is an important component of bed sites. We believe our results may have been influenced by a preponderance of taller grasses, such as wheatgrasses (*Agropyron* spp.), whose culms contribute to vegetation height but not as much to vegetation density.

With the exception of VOR, our results, emphasizing adequate herbaceous growth at fawn bed sites, are generally supported by other studies. Hyde et al. (1987) determined that percent canopy cover of grasses and forbs is greater at bed sites than on random sites Huegel et al. (1986) also found that mean percent canopy cover of most herbaceous components is greatest at bed sites, but there were fewer tall grasses and low and medium forbs in that study.

Fawns in our Black Hills study used areas having less tree canopy cover ($P \le 0.001$), but use differed between years ($P \le 0.001$; Figs. 3a, b). Fawn use of areas with less mean tree cover, apparent only from mid-June to early August 1991, lasted all season in 1992. Mean percentage tree cover averaged 28.8 ± 0.7% and 20.5 ± 0.6% at fawn bed sites and 36.4 ± 0.6% and 39.4 ± 0.6% at random sites in 1991 and 1992, respectively. Fawns also used bed sites with lower ponderosa pine basal area ($P \le 0.001$), but because use did not differ between years ($P = 1.000$), we combined years (Fig. 4a). Fawn bed sites contained a mean pine basal area of 11.0 ± 0.4 m^2/ha, while random sites averaged 16.5 ± 0.2 m^2/ha.

Changes in tree cover, especially ponderosa pine overstory, directly affect understory development in the Black Hills (Uresk and Severson 1989). Fawns used relatively tall, dense, grass-dominated herbaceous vegetation for bed sites, and the best opportunities were under thinned pine stands. Uresk and Severson (1998) reported that total grass production is nearly twice as great under pine stands stocked at 9 m^2/ha than at 14 m^2/ha basal area. Further, grass species that decrease most rapidly with increasing pine basal area are the taller ones, such as wheatgrasses. Herbaceous species capable of providing adequate fawn cover are virtually absent in ponderosa pine stands with basal areas above 14 m^2/ha (Uresk and Severson 1998).

Fawn use of ponderosa pine forest in the Black Hills may be somewhat unique to the area within which this study was conducted. Pine is dominant throughout, occurring on 91.1% of random sites; aspen, the next most abundant species, is found on only 32.9% of random sites. In an earlier study in the northwestern portion of the Black Hills, Kennedy (1992) concluded that closed deciduous habitats (aspen and aspen/birch) are important for providing feeding and loafing sites and optimum hiding and security cover for does during fawning. His study focused on the dam and not the fawn, but the area did contain extensive aspen stands of varying ages. Our data indicate fawns use areas with less aspen basal area ($P = 0.013$) than that found in random sites (Fig. 4b). In our study area aspens often are scattered within some white spruce and more mesic pine stands. Small patches or stringers of aspen occur, but only in the bottoms

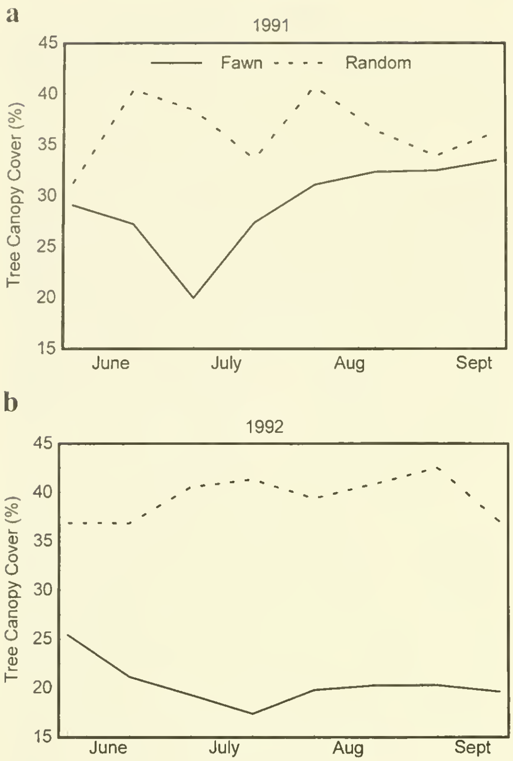

Fig. 3. Tree canopy cover (%) at white-tailed deer fawn bed sites versus random sites in 1991 (a) and 1992 (b) from early June to late September, Black Hills, South Dakota. Significant at $P = 0.10$.

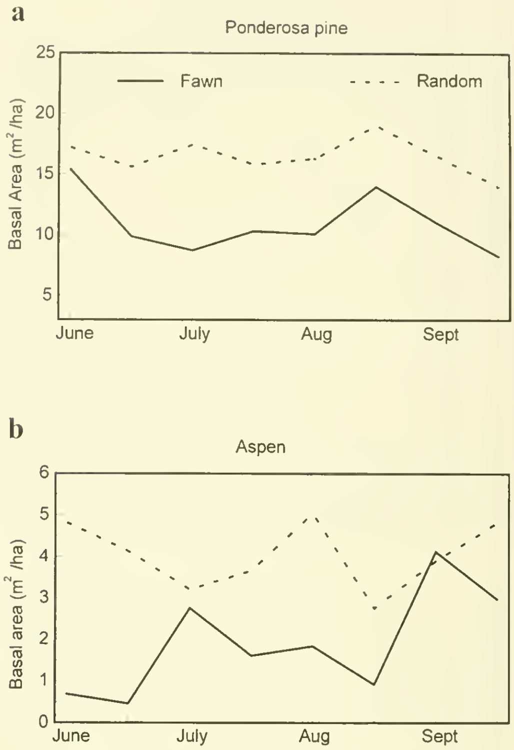

Fig. 4. Basal area (m^2/ha) at white-tailed deer fawn bed sites versus random sites for ponderosa pine (a) and aspen (b) from early June to late September 1991 and 1992 combined, Black Hills, South Dakota. Significant at $P = 0.10$.

of upper drainages or as a narrow, discontinuous, transitional band between open meadows and the pine forest. Extensive, continuous aspen stands as described by Kennedy (1992) do not occur in our study area.

Slash was more prevalent at bed sites than random sites ($P = 0.054$). This may be related to seasonal development of the herbaceous understory. Understory in the Black Hills is not fully developed in early June, and early fawns may have had to use alternative cover types. Most differences occurred during June (except for the first 2-wk period) and the first 2 wk in July, but not after mid-July (Fig. 5a).

Fawns used bed sites with less shrub cover ($P \leq 0.001$) than at random sites (Fig. 5b). Other studies of white-tailed deer fawn bed sites reached different conclusions regarding woody vegetation. Bed sites contained more woody cover than did random sites in Iowa (Huegel et al. 1986) and southern Texas (Hyde et al. 1987). Mean shrub cover averaged 22 ± 14% at Black Hills fawn bed sites compared to 31 ± 14% at random sites. Further, nearly half the shrub cover, 11% on fawn bed sites and 13% on random sites, was composed of mat-forming (e.g., bearberry) or low-growing (e.g., Oregon grape) shrubs that contribute little to fawn hiding or thermal cover. Taller woody shrubs, with few exceptions, are not a substantial part of the total landscape.

Lack of shrubs tall enough to hide a reclining fawn is a common feature of ponderosa pine understory in portions of the central (Uresk and Severson 1989) and northeastern Black Hills. Thilenius (1972) noted that the 2 most common habitat types in the northeastern Black Hills lack a tall shrub stratum. Twenty-two tall shrub species (including tree seedlings) occur on the study area. Seventeen average <1.0% cover, which indicates limited, scattered distributions. Extensive tall shrub patches are rare. Most common are dense patches of western snowberry (*Symphoricarpos*

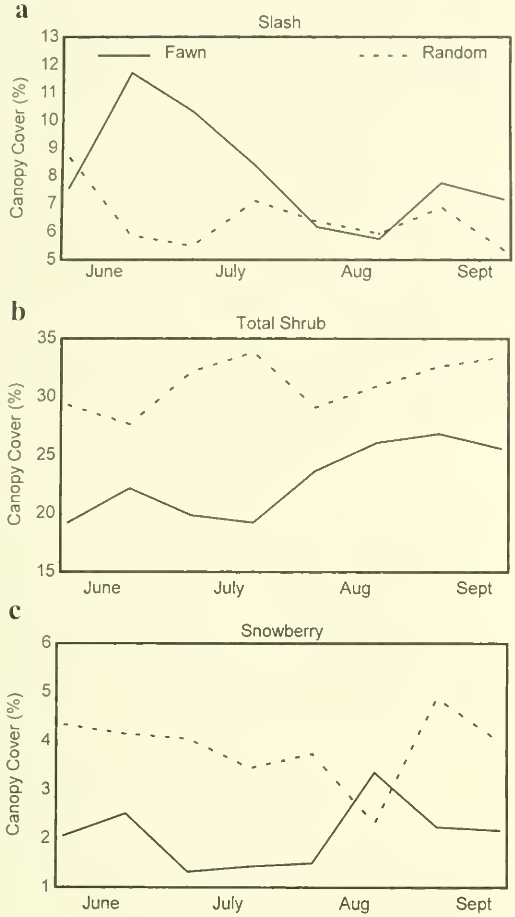

Fig. 5. Canopy cover (%) of slash (a), total shrubs (b), and snowberry (c) at white-tailed deer fawn bed sites versus random sites from early June to late September 1991 and 1992 combined, Black Hills, South Dakota. Significant at $P = 0.10$.

occidentalis), which probably forms an impenetrable barrier to fawns or focal points for searching predators. These shrub patches were avoided ($P \leq 0.001$), at least during the early part of the season when fawns were small (Fig. 5c).

MANAGEMENT IMPLICATIONS

The few studies about bed site use by white-tailed deer fawns have revealed differences in kinds of cover used, but all have generally agreed, including ours, that sites chosen by fawns are characterized by having more vertical and horizontal obstruction for screening cover than those found on randomly selected sites. We concur with Huegel et al.'s (1986) statement that fawns select bed sites in different habitats seemingly irrespective of the plant species present. In this study selection was related to understory structure. In the northeastern Black Hills, bed sites were found in relatively open stands of ponderosa pine (basal areas about 11 m^2/ha) with a substantial percentage of grass cover (32%) and a relatively tall understory. Such conditions could be achieved by silvicultural treatments in pine stands in the northern and central Black Hills that leave residual basal areas <11 m^2/ha (Uresk and Severson 1998). However, the southern Black Hills are drier, with different soils and possibly some understory differences. Current timber harvest standards and guidelines, however, call for growing basal area levels ranging from 14 m^2/ha to 18 m^2/ha (Black Hills National Forest 1983), which are similar to basal area levels of our randomly selected sites.

Management prescriptions are confounded when the dam's habitat use patterns are considered. The dam apparently chooses the macrohabitat type where the fawn is left, but the fawn selects the actual bed site (Marchinton and Hirth 1984, Heugel et al. 1986). The dam then feeds and loiters at distances from fawns that can range from 75 to 230 m (Huegel 1985 as reported in Schwede et al. 1994). Habitats used by fawns as bed sites could logically be different from those used by dams as described by Kennedy (1992) and Stefanich (1995) for the northwestern Black Hills. We cannot, therefore, make specific recommendations regarding adult female habitats from this study.

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RESPIRATION CHARACTERISTICS DIFFER AMONG CHEATGRASS (*BROMUS TECTORUM* L.) POPULATIONS

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ABSTRACT.—Cheatgrass (*Bromus tectorum* L.) is a dominant weed that has increased the frequency of wildfire in the Great Basin since its introduction about 100 yr ago. This study examines characteristics of respiratory metabolism in several different populations. Seeds from 6 populations were germinated and metabolic heat rates (q) and dark respiration rates (R_{CO_2}) of all seedlings were measured calorimetrically at 15° and 25°C or (for 3 populations) at 5° intervals from 5° to 35°C. Growth rates, substrate carbon conversion efficiencies, and Arrhenius temperature coefficients were calculated from the data. Results show that cheatgrass metabolism is most efficient at temperatures near 0°C; at temperatures above 20–25°C, efficiency goes to zero. Cheatgrass populations differ in their temperature dependencies of substrate carbon conversion efficiency and predicted growth rate. Measurements of respiratory heat and CO_2 rates as functions of temperature can be made relatively quickly and used to aid understanding of metabolic adaptation by invasive and native species to the environment.

Key words: Bromus tectorum, *calorimetry, cheatgrass, growth, respiration, temperature.*

The annual grass *Bromus tectorum* was introduced into western North America in the late 19th century and is now a dominant plant in many areas including the Great Basin (Mack 1981). Alteration of the wildfire cycle has contributed to this invasion. Before European settlement, areas of the Great Basin experienced wildfires once each 32–70 yr, but now, because of cheatgrass, many areas have wildfires every 3–5 yr (Whisenant 1990). More frequent burns accelerate conversion of vegetation from shrubs to annual grasses.

Because frequent burning is counterproductive and areas of cheatgrass are too extensive for mechanical or chemical control, the best possibility for controlling cheatgrass is to find plants that can compete effectively with this weed (Pellent 1990). Cheatgrass is a predominantly self-pollinating winter annual. Seeds ripen and disperse in early summer but do not germinate until autumn (Beckstead et al. 1996). Germinated seedlings overwinter and continue growth in the very early spring, then flower and set seed by early June. Because most precipitation in the Great Basin is winter snow, cheatgrass can effectively use winter–spring moisture to outcompete rival summer-active species.

Seed maturation and germination differences among populations of cheatgrass are known adaptations to particular sites (Beckstead et al. 1996), and such differences have a genetic basis (Novak et al. 1991). Among populations of other species, differences in photosynthesis, water-use efficiency, and respiration have been documented (Tilman 1993). This study shows that respiratory characteristics differ among populations of cheatgrass. Two measures of respiration rate, CO_2 evolution rate and metabolic heat rate, and their temperature dependencies were determined and used to calculate growth rate and efficiency of converting photosynthate to structural carbon, both as functions of temperature (Hansen et al. 1994).

Increased understanding of adaptation of cheatgrass metabolism to environmental temperature may provide a basis from which to begin selecting populations of other species that can compete effectively with cheatgrass early in the growing season. Other properties of the environment, e.g., growth season, water availability, soil type, and mineral exchange

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TABLE 1. Origin of *Bromus tectorum* used in this study.

Location	Community type	Elevation
(1) St. George, UT	creosote bush scrub	ca 850 m
(2) Hobble Creek Canyon, Springville, UT	mountain brush	ca 1280 m
(3) Potosi Pass, near Las Vegas, NV	blackbrush	ca 1280 m
(4) Whiterocks Rd., near Dugway, UT	shadscale, Wyoming big sagebrush	ca 1450 m
(5) Strawberry Reservoir, UT	mountain meadow	ca 2290 m
(6) Fairview Rd., Manti-LaSal National Forest, UT	aspen/fir	ca 2520 m

capacity, and physiological parameters other than those included in this study are also important but are not considered here.

MATERIALS AND METHODS

Cheatgrass seed from 6 different populations (Table 1) was provided by the USDA Forest Service Shrub Sciences Laboratory in Provo, Utah. Seed used in the 1st part of this study was harvested from all 6 populations immediately following the 1992 growing season. Seed was also collected in 1995 from greenhouse-grown progeny of 10 maternal lines each of 3 populations and used for a more extensive 2nd set of measurements.

Cheatgrass seed was germinated at room temperature in normal room light on wet filter paper in petri dishes. Measurements were made on whole seedlings, 5–8 d old. Several previous studies have shown data on seedlings predict vegetative growth rates of older plants (Anekonda, Criddle, and Hansen 1994, Anekonda, Criddle, Libby et al. 1994, Criddle et al. 1995, Monaco et al. 1996, Smith et al. 1996, Taylor et al. 1998).

All data were collected with Hart Scientific model 7707 differential, heat conduction, temperature-scanning calorimeters operated in the isothermal mode according to published procedures (Criddle et al. 1991, Hansen et al. 1996). Baseline corrections were made with data taken on empty ampules. Specific metabolic heat rates, q (μJ s^{-1} mg dry wt^{-1} or μW mg dry wt^{-1}), and dark respiratory CO_2 rates, R_{CO2} (pmol s^{-1} mg dry wt^{-1}), were calculated from the measurements. Tissue was dried overnight at 70°C in a vacuum oven for dry weight. Measurements of q and R_{CO2} were made at 15° and 25°C on 6 populations from seed collected in 1992 and at 5, 10, 15, 20, 25, 30, and 35°C on 3 populations from seed collected in 1995. Three or 4 (typically 3) seedlings were used for each measurement, and several replicates were performed and averaged at each temperature.

Heat rate (q) for each sample was first obtained at a given temperature; then a 50-μL vial containing 40 μL of 0.4M NaOH was placed in the 1-mL calorimeter ampule and total heat rate measured. This was followed by another measurement of q for the sample. The difference between heat rates with and without NaOH, divided by the enthalpy change for the reaction of CO_2 with NaOH(aq) to produce HCO_3^- (–108.5 kJ mol^{-1}), gives R_{CO2} (Criddle et al. 1991, Hansen et al. 1996). The ratio of q/R_{CO2} was calculated for individual samples and then averaged for replicate experiments on a population. Slope of an Arrhenius plot (ln q vs. T^{-1} in reciprocal kiloKelvins) of averaged q data is equal to μ_q, temperature dependence of q. Temperature dependence of R_{CO2}, μ_{CO2}, is the slope of the Arrhenius plot (ln R_{CO2} vs. T^{-1}) for the averaged R_{CO2} data.

Model

The model proposed by Hansen et al. (1994, 1996) is used to interpret the data obtained. Specific growth rate R_{SG} (pmol C s^{-1} mg dry wt^{-1}), i.e., rate of conversion of substrate carbon to biomass carbon, as given by this model is equation 1,

$$\begin{aligned} R_{SG} &= [-q - R_{CO2}(1 - \gamma_p/4)\Delta H_{O2}]/\Delta H_B \\ &= R_{CO2}(\varepsilon/[1 - \varepsilon]) \end{aligned} \qquad (1)$$

where q is specific metabolic heat rate, R_{CO2} is specific CO_2 rate, γ_P is mean oxidation state of the substrate carbon, ΔH_{O2} is a constant equal to -455 ± 15 kJ mol^{-1}, ΔH_B is enthalpy change for conversion of substrate to biomass, and ε is substrate carbon conversion efficiency. In the calculations done in this study, γ_p was assumed equal to zero (i.e., substrate C was assumed to be carbohydrate). ΔH_B was assumed to be constant, but no value was assumed because ΔH_B was not separated from R_{SG} or the ε function. Thus,

$$R_{SG}\Delta H_B = 455R_{CO2} - q \qquad (2)$$

In the range of temperatures where the Arrhenius equation describes temperature dependence of respiration rates, substitution of the Arrhenius equation ($R = Ae^{-\mu/T}$, where A is a constant, μ is Arrhenius temperature coefficient, and T is absolute temperature) for the temperature-dependent variables in equation 2 gives

$$R_{SG}\Delta H_B = [-A_q e^{-\mu q/T} + 455A_{CO2}e^{-\mu CO2/T}] \qquad (3)$$

where μ_q is temperature coefficient for metabolic heat rate, μ_{CO2} is temperature coefficient for CO_2 rate, and temperature is absolute temperature in Kelvins. Equation 3 thus predicts how temperature affects R_{SG} from short-term, rapid measurements.

The product $R_{SG}\Delta H_B$ is the predicted specific growth rate in terms of rate of energy storage in new structural biomass with substrate as reference. Ratio of metabolic heat rate to CO_2 rate is related to ε, substrate carbon conversion efficiency, by the model as

$$q/R_{CO2} = 455 - [\varepsilon/(1 - \varepsilon)]\Delta H_B \qquad (4)$$

Temperature dependence of q/R_{CO2} and thus of ε (assuming ε is the only temperature-dependent quantity on the right side of equation 4) is given by

$$q/R_{CO2} = [-A_q e^{-\mu q/T}]/[A_{CO2}e^{-\mu CO2/T}] \qquad (5)$$

RESULTS

Values of q and R_{CO2} measured at 15° and 25°C on seedlings grown from seed collected in 1992 are presented in Table 2. Because of within-population (genetic) biodiversity, standard deviations of mean values in Table 2 are larger than in other studies we have done with clones and cultivars, where relative uncertainties are generally <10%. Therefore, several (~10) replicates were run to properly characterize the population; i.e., each mean is the average for 30–40 seedlings.

Figure 1 represents extrapolations of q and R_{CO2} data at 15° and 25°C according to the Arrhenius equation. Slopes of lines shown in Figure 1 are $-\mu_q$ and $-\mu_{CO2}$ values. Temperature effect on q is much greater than for R_{CO2} in all cases. The ratio q/R_{CO2} thus increases rapidly with temperature, predicting a rapid decline in substrate carbon conversion efficiency as temperature increases (Fig. 2). While μ_q varies among populations, it is less variable than μ_{CO2}.

Figure 2 shows curves of $R_{SG}\Delta H_B$ values as a function of temperature as calculated from equation 3. In agreement with directly observed growth characteristics, Figure 2 predicts rapid growth of cheatgrass at cool temperatures and decreasing growth rate as temperatures rise. Based on predicted behavior at temperatures

TABLE 2. Specific dark respiratory heat (q) and CO_2 rates (R_{CO2}) [$\pm s_{\bar{x}}$] measured at 15°C and 25°C for seedlings of *Bromus tectorum* from 1992 seed collection. Number of measurements is given in parentheses. Three to 4 seedlings were used for each measurement.

Accession	q at 15°C $\mu W\ (mgDW)^{-1}$	q at 25°C $\mu W(mgDW)^{-1}$	R_{CO2} at 15°C $pmol(mgDW)^{-1}s^{-1}$	R_{CO2} at 25°C $pmol(mgDW)^{-1}s^{-1}$
St. George	5.1 ± 2.2(12)	11.7 ± 4.1(14)	18.8 ± 13.9(12)	24.8 ± 10.1(14)
Hobble Creek	6.7 ± 2.5(11)	12.7 ± 4.6(13)	23.4 ± 10.9(11)	36.1 ± 14.6(13)
Potosi Pass	4.6 ± 3.3(11)	10.2 ± 4.3(11)	24.4 ± 32.2(11)	24.7 ± 14.0(11)
Whiterocks	5.6 ± 1.3(9)	12.7 ± 4.2(12)	21.5 ± 11.8(9)	25.6 ± 6.0(12)
Strawberry	5.6 ± 1.8(14)	10.5 ± 3.9(10)	25.4 ± 19.2(14)	26.4 ± 11.6(10)
Fairview	5.8 ± 1.5(8)	12.3 ± 4.4(10)	24.4 ± 7.0(8)	30.3 ± 11.7(10)

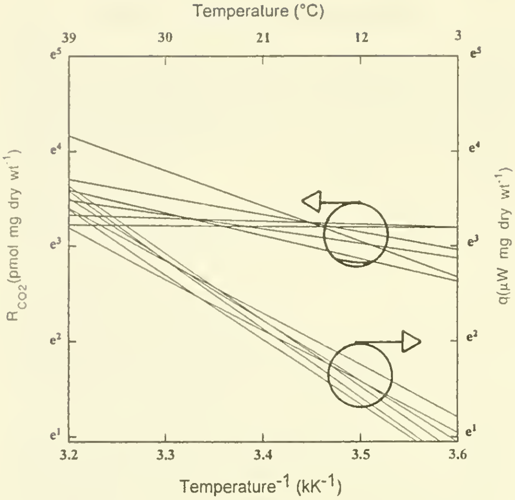

Fig. 1. Arrhenius plot for q (lower lines) and R_{CO2} (upper lines) showing differences in temperature dependence among 6 populations of *Bromus tectorum*.

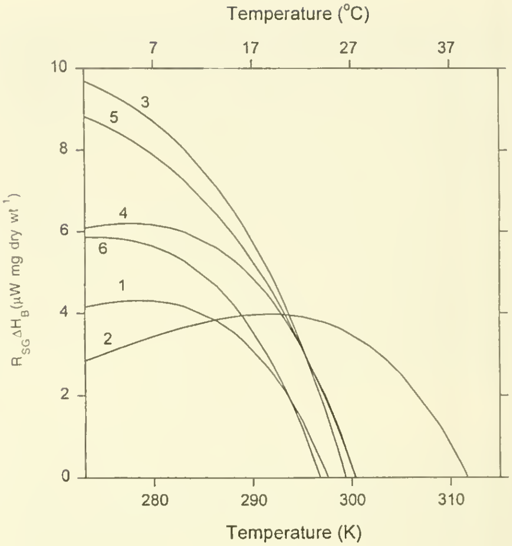

Fig. 2. Plot of calculated relative specific growth rates among 6 populations of *Bromus tectorum* (see equation 2): St. George (1), Hobble Creek (2), Potosi Pass (3), Whiterocks (4), Strawberry Reservoir (5), and Fairview (6).

above approximately 20°C, the 6 populations fall into 3 groups. The 1st group (St. George [1] and Fairview [6]) has the lowest maximum temperature allowing growth. The 2nd group (Potosi [3], Whiterocks [4], and Strawberry [5]) is predicted to be capable of growth at slightly higher temperatures. The Hobble Creek (2) population will survive and grow at much higher temperatures but is much slower growing at low temperatures.

R_{CO2} and q data were obtained at 7 temperatures for a representative of each of these 3 groups (St. George, Potosi, and Hobble Creek) from maternally known parents. Growth rates and efficiencies calculated from these data are plotted in Figures 3 and 4. Because the slope of the Arrhenius plot of data taken below 15°C was very different from that for data at and above 15°C, data were treated as 2 sets and fit to separate Arrhenius equations. For these 3 populations from the 1995 seed, predicted specific growth rate for the St. George population was highest at cool temperatures and lowest at warmer temperatures. Based on temperatures at which calculated curves cross zero, St. George plants would probably not grow above 20°C, while Potosi and Hobble Creek plants would grow at temperatures to about 25°C. Data in Figure 3 are thus in essential agreement with curves in Figure 2 extrapolated from a much narrower range of data.

Efficiency curves given in Figure 4 exhibit much the same temperature dependence as growth rate curves shown in Figure 3, thus showing that temperature dependence of efficiency is the major determinant of temperature dependence of growth rate; that is, even though metabolic rate increases with temperature, efficiency decreases even faster.

DISCUSSION

Results shown in Figures 2 and 3 correlate with cheatgrass growth strategy which, in general, is to germinate in fall, overwinter in a vegetative state, and then grow rapidly in early spring when temperatures are still cold. Figure 2 indicates the Hobble Creek population from 1992 seed had a growth response to temperature significantly different from other populations. Cheatgrass grows very well in the mouth of Hobble Creek Canyon during late winter and early spring when below-freezing nighttime temperatures are common. However, 30–35°C daytime temperatures can also occur during the same time period. Seedlings from the Hobble Creek population grown from more genetically uniform seed collected in 1995 were not as different from the other

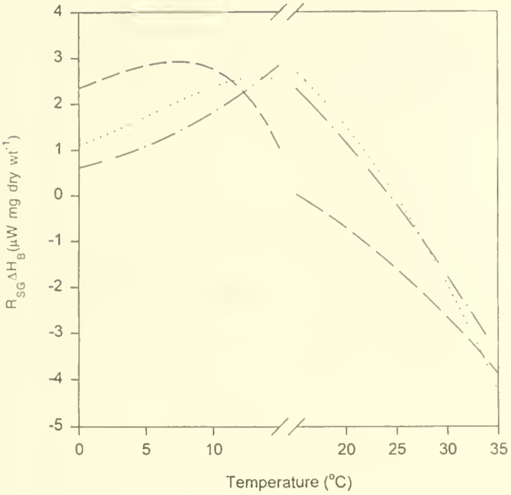

Fig. 3. Plot of temperature dependence of calculated relative specific growth rates for 3 populations of *Bromus tectorum* using 1995 seed (see equation 2) from St. George (_ _ _ _), Hobble Creek (. . . . . .), and Potosi Pass (_ . _ . _ .) populations.

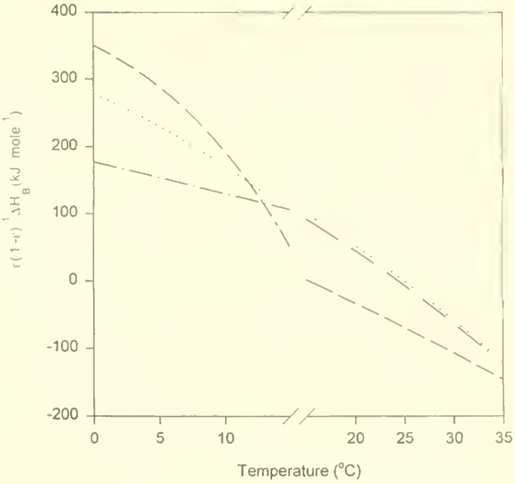

Fig. 4. Plot of carbon conversion efficiency versus temperature for 3 populations of *Bromus tectorum* (see equation 4). Symbols as in Figure 3.

populations (Fig. 3). These results may reflect a climatic selection of annual selfed seeds.

Our results indicate that cheatgrass populations are distinguished from one another by metabolic phenotypes defined by temperature dependencies of q and R_{CO2}. Earlier, Novak et al. (1991) reported genetic differences between populations of cheatgrass. Temperature dependencies of growth rate and substrate carbon conversion efficiency, and thus site fitness of a population, are determined by the difference between μ_q and μ_{CO2}, which in turn is related to the biochemistry of metabolism (Taylor et al. 1998). These data on seedlings should be representative of metabolism in field plants because, during measurement, seedlings were metabolizing stored substrate with normal dark respiratory pathways at temperatures not damaging to tissues. Under these conditions about 90% of metabolic heat is generated from reduction of oxygen in mitochondria (Hansen et al. 1997) by carbohydrate from stored substrates. CO_2 is generated mostly in mitochondria, but some comes from the pentose phosphate shunt. For q and R_{CO2} to have different temperature dependencies, reactions producing heat and CO_2 cannot be stoichiometrically linked. This in turn requires a change in the coupling of ATP synthesis to oxidative reactions with temperature. Therefore, differences in temperature dependencies of q and R_{CO2} between populations are genetically determined and do not represent acclimation.

Application of techniques used in this study to other species could be used to rapidly determine if another species has the potential to outgrow cheatgrass at temperatures similar to those conducive to cheatgrass growth. If potential competitor species can be identified, then field tests and competition trials could be used much more efficiently.

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CAUDAL DISTRACTION BY RAT SNAKES (COLUBRIDAE, *ELAPHE*): A NOVEL BEHAVIOR USED WHEN CAPTURING MAMMALIAN PREY

Stephen J. Mullin[1]

ABSTRACT.—Caudal movement in snakes may serve either a predatory (e.g., caudal luring) or defensive (e.g., rattling, aposematism) function. I describe a new behavioral pattern of tail movement in snakes. Gray rat snakes (*Elaphe obsoleta spiloides*) foraging on small mammals (*Mus domesticus*) moved their tails in an erratic, whiplike fashion after detecting prey in their vicinity. The thrashing movement in the horizontal plane was audibly and visually obvious, resulting in displacement of leaf litter around the tail. All subjects displayed the behavior, but not in all foraging episodes. Shorter durations of caudal distraction resulted in greater predator success during the 1st attempt at prey capture. Caudal distraction may facilitate prey capture by gray rat snakes by directing the attention of prey away from the approaching head of the snake.

Key words: caudal display, predatory behavior, deceit, Elaphe obsoleta, *mammalian prey, rat snake, Colubridae.*

Visual communication by snakes (Carpenter 1977, Carpenter and Ferguson 1977) occurs in the absence of appendages used by many other vertebrate taxa (Cullen 1972, Enquist et al. 1985). Limblessness necessitates the use of head, body, or tail for visual display. Snake defensive displays frequently involve tail movement or posturing (Greene 1988, Sazima and Abe 1991). In particular, members of the subfamily Crotalinae have evolved a specialized morphology at the tail tip, the rattle. Greene (1992) suggested that the incipient structure serves as a warning device to snake predators, a conclusion that is the subject of continued discussion (Sisk and Jackson 1997, Tiebout 1997). Several species of colubrid snakes (Greene 1988) and other elongate reptiles (Greene 1973) also perform defensive tail displays.

Another form of tail movement, termed *caudal luring*, facilitates prey capture. This behavior is described as a slow, undulatory or vermiform movement of the tail while it is held upright in close proximity to the snake's head (Heatwole and Davison 1976). Caudal luring is presumably mimetic, in that the movement is thought to resemble an insect larva or worm and thus attracts potential prey to within striking distance of the otherwise motionless snake. Caudal luring has been documented in nearly all families of snakes (Carpenter et al. 1978, Radcliffe et al. 1980, Sazima and Puorto 1993, Rabatsky and Farrell 1996) and at least 1 lizard species (Murray et al. 1991). It is typically displayed by snakes foraging from an ambush posture (Chiszar et al. 1990).

Both defensive tail vibration and caudal luring have been observed in rat snakes (*Elaphe obsoleta*; Tiebout 1997; personal observation). While observing a gray rat snake (*E. o. spiloides*) foraging for a small mammal (*Mus domesticus*), I recorded a tail display unlike that of either luring (Chiszar et al. 1990) or defensive rattling or tail vibration (Greene 1988). During subsequent observations, several individuals displayed similar tail movement when approaching their prey. The purpose of this study is to describe a heretofore undocumented predatory behavior of gray rat snakes that was displayed only in the presence of mammalian prey. Frequency and duration of this behavior and its facilitation of prey capture are also reported. Because this behavior parallels caudal luring and defensive tail vibration, I term the novel behavior *caudal distraction*.

MATERIALS AND METHODS

I first noticed caudal distraction in a 113-cm snout-vent length (SVL) female gray rat snake foraging for a mixed-strain mouse (*M. domesticus*). The snake was in an enclosure that simulated a bottomland hardwood forest habitat (see below). Behavior was documented on videotape to permit detailed description. Several other adult snakes displayed this behavior with little departure from the original pattern. To examine possible differences in capture success and latency to prey capture that might be dependent on the use of this behavior, I recorded adult gray rat snakes ($n = 15$) involved in foraging episodes under similar conditions.

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Subjects (10 males and 5 females, ≥100 cm SVL) were obtained from forested and semirural areas within Shelby County, Tennessee, and maintained in captivity at temperature and photoperiod regimes of 26–29°C and 14:10 h light:dark, respectively. Subjects had spent between 1 and 16 months in captivity prior to examination. Snakes were housed individually in cages measuring a minimum of 30 × 60 × 30 cm, provided with water ad libitum, and fed either Northern Bobwhite Quail (*Colinus virginianus*) eggs or mixed-strain mice weekly. Excepting occasional cage cleaning and monthly SVL (±0.5 cm) measurements, subjects were handled as little as possible to minimize any behavioral modifications resulting from prolonged captivity (Warwick 1990, Ford 1995). Because recently fed snakes may exhibit shifts in behavioral pattern (Beck 1996) or alteration of locomotor performance (Martin 1996), individuals were placed on a restricted diet (water alone) for 3 wk prior to experimental trials. Between 23 April 1995 and 25 March 1996, snakes were allowed to forage individually for mice on at least 2 different occasions, each separated by a 3-wk restricted diet.

An enclosure (2.25 m^2 and 2 m in height), constructed to simulate bottomland hardwood forest of the wildlife management area of nearby Meeman-Shelby Forest State Park (MSFSP), Tennessee, was maintained at the photoperiod and temperature regimes described above. Artificial vegetation simulated mean recorded level of vegetation density at MSFSP (measured in June 1994; $\bar{x} \pm 1\ s_{\bar{x}} = 64 \pm 2.3$ plants m^{-2}, $n = 144$). Leaves, obtained at field sites where snakes were collected, provided a natural substrate on the enclosure floor. Light intensity on the enclosure floor approximated levels measured at MSFSP during the vegetation sampling period (for further details on habitat sampling and enclosure construction, see Mullin 1998, Mullin et al. 1998).

Adult male mice were placed in the enclosure for a minimum of 10 min for acclimatization. Only adult male mice having dark brown pelage were used as prey during the observations to minimize visual and vomeronasal differences among prey available to snakes (Loop 1970) and provide prey visually similar to those which snakes encounter in the field. All mice had similar mass (30.7 ± 0.5 g, $n = 30$), although the ratio of prey mass to snake mass was not fixed during the study. A gray rat snake was placed in the corner of the enclosure farthest removed from the prey. Because observer presence may influence snake behavior (Drummond 1983), behaviors were recorded by a video camera on a tripod elevated over the enclosure floor. The camera was always oriented toward the snake, meaning that possible differences in prey behavior were not recorded. Occasionally, caudal distraction was initiated with the tail outside the field of view; however, tail movement was audibly discernible as leaf litter in the immediate vicinity was disturbed and could thus be recorded from its initial occurrence.

The latency to successful mouse capture may have depended, in part, on initial distances separating the snake and its prey. However, the confined, relatively small enclosure probably limited the influence of initial separation distance. Missed attempts at capturing the mouse and frequency and duration of caudal distraction were recorded from videotaped observations. A repeated-measures analysis of variance (ANOVAR; each subject was recorded on 2 occasions) was used to determine whether those snakes exhibiting caudal distraction required fewer attempts to successfully capture mice. Parametric statistics (Scheffé 1959, Cohen 1965) were also used to detect any relationships between frequency and/or duration of caudal distraction and snake gender (ANOVAR) or size (Pearson's regression). Statistical tests were conducted using SuperANOVA™ software (Abacus Concepts) at an accepted significance level of $\alpha = 0.05$.

RESULTS

Description

Caudal distraction is the use of tail movements by an elongate predator which serve to hold the attention of a prey animal while the predator's head is moved to within striking range of the prey.

In *E. o. spiloides* caudal distraction displaced leaves near the tail, was visually conspicuous when unobscured by emergent vegetation, and was audible from a distance of several meters. Mice (*M. domesticus*) responded to caudal distraction by ceasing all movement, often after orienting their heads toward the undulating tail (Fig. 1). An erratic lateral movement of the posterior 70% of the tail characterized the tail display. Undulations of the more proximal tail portion appeared sinusoidal in form, but the tail tip moved similarly to the end of a whip, curving in a 180° arc on either side of the tail. Such movements were serially repeated with an average ($\pm 1\ s_{\bar{x}}$) of 1.4 ± 0.2 sec elapsing for each whiplike pattern. Usually, but not always, caudal distraction was performed while the body was laterally bent at an obtuse angle such that tail movement was positioned to one side of the body axis with respect to the head. Differences between caudal distraction and other described tail movements are discussed below.

All 15 gray rat snakes displayed the described behavior, although not in all foraging episodes (caudal distraction was observed in 19 of 30 staged encounters and has been documented in >20 other occasions involving these and other adult subjects foraging in different enclosure conditions; Mullin 1998). The behavior, while most often displayed after snakes visually detected mice, also occurred when prey was visually obscured (possibly a response to tactile or chemosensory stimuli). Caudal distraction was always initiated before the head of the snake was within striking distance of its prey (<10 cm). Duration of the behavior always extended to the moment of striking the prey. Subjects displaying caudal distraction did not require less time (127 ± 32 sec) to capture prey than those not displaying the behavior (140 ± 36 sec; $F_{1,13} = 0.09$, $P = 0.70$). Subjects did not display caudal distraction when offered other prey types (*Colinus virginianus* and *Coturnix coturnix* eggs, *C. virginianus* chicks, *Hemidactylus turcicus* juveniles, *M. domesticus* neonates) under similar test conditions.

Displays ($n = 19$) averaged 27 ± 8 sec in duration and were usually initiated while the snakes were actively searching for prey, or less often from a stationary position (although not necessarily a coiled posture). Snakes were rarely stationary for the entire duration of a caudal distraction display; instances of stationary caudal distraction were frequently accompanied by some time displaying the behavior while advancing toward the mouse. There was no difference in the amount of time a snake displayed caudal distraction as a function of foraging mode (ambush or pursuit) or trial order ($F_{1,13} \leq 1.93$, $P \geq 0.19$).

The ability of gray rat snakes to capture their prey on the 1st strike was influenced by the duration of caudal distraction (Table 1; Pearson's $r = 0.71$, $P = 0.003$); longer times spent performing caudal distraction were associated with fewer successful 1st strikes. Snakes failing to capture their prey on the 1st attempt typically succeeded on the 2nd or 3rd strike. Neither frequency nor duration of caudal distraction was a function of snake gender ($F_{1,13} < 0.1$, $P \geq 0.9$) or size (Pearson's $r < 0.31$, $P \geq 0.26$). There was no difference in rate of successful capture on the 1st attempt as a function of whether the snake displayed caudal distraction while moving or stationary ($F_{1,13} = 0.15$, $P = 0.71$).

DISCUSSION

Caudal distraction most closely resembles rapid tail movements that Carpenter et al. (1978) described as part of the caudal luring sequence in death adders (*Acanthophis*). However, caudal distraction differs from luring in 2 discernible features: (1) position of the tail relative to the snake's head—distance separating head and tail is greater when distracting than when luring, with the tail displaced laterally away from the head (rather than aligned in front of, or behind, the head); and (2) speed of tail movement—distraction movements are generally faster than movements described for luring (approaching 2 undulations sec^{-1}; Carpenter et al. 1978).

Caudal distraction was always initiated before snakes were within striking distance of their prey, and mice typically directed their attention toward the tail. When using caudal distraction, snakes approached prey more slowly than when not displaying the behavior. Although striking distance in foraging episodes was not quantified in this study, the behavior may permit closer approach of snakes to their prey prior to attempting capture (Schmidt et al. 1993). Foraging attempts involving display of caudal distraction did not result in gray rat

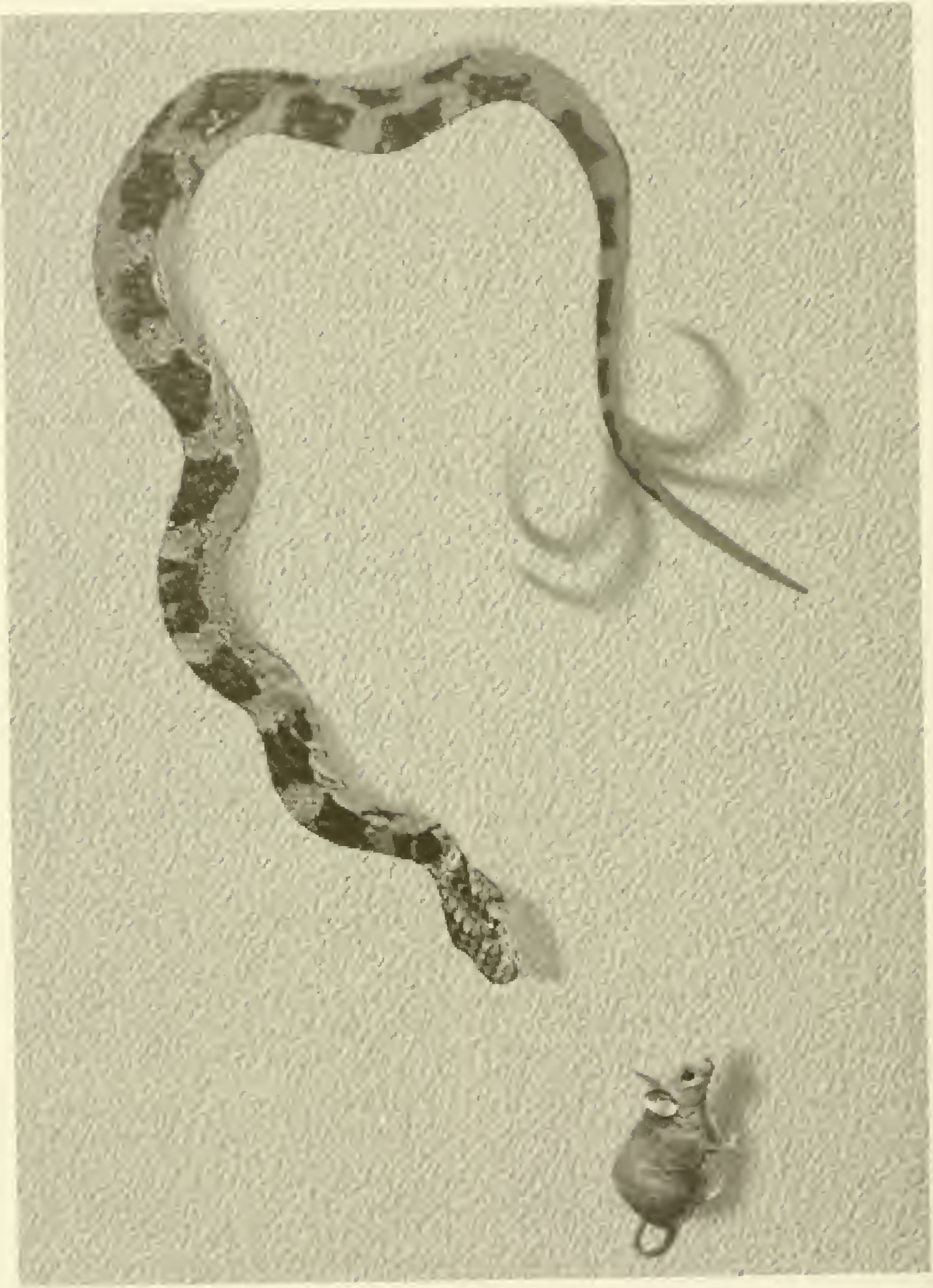

Fig. 1. Caudal distraction in *Elaphe obsoleta spiloides* (digitized from videotaped observations). Blurred silhouettes of tail indicate maximum curvature of tail during performance of behavior.

TABLE 1. Capture success as a function of the duration (sec; mean ± 1 $s_{\bar{x}}$) of caudal distraction display in adult gray rat snakes (*Elaphe obsoleta spiloides*). Sample sizes are given in parentheses. Values in 2nd and 3rd columns are different (Pearson's $r = 0.71$, $P = 0.003$).

Duration of caudal distraction	Duration of caudal distraction when 1st strike succeeded	Duration of caudal distraction when 1st strike failed
27 ± 8 (19)	11 ± 7 (14)	59 ± 14 (5)

snakes requiring less time for successful prey capture.

Two concerns are pertinent to the occurrence of caudal distraction in gray rat snakes (Wickler 1968, Greene and Campbell 1972): (1) whether prey respond to the behavior as they would to a potential food item (a deception) and therefore approach the snake, or are distracted by it (thereby facilitating approach of the snake to within striking distance); and (2) whether the behavior occurs only during periods of hunger, or as a nervous response to an unrecognized object.

In answer to the initial concern, mice directed their attention toward the tail display but never approached the area of leaf litter being disturbed by the display. The only occasions (*n* = 3) when a mouse was observed in the area of a snake's tail were before caudal distraction had been initiated, presumably because the snake had not yet detected its prey. Subjects displaying caudal distraction for a longer duration before attempting to capture their prey were less likely to succeed on their 1st strike. Although these situations could have involved mice that were inherently warier (other than excluding those with discernible physical or behavioral aberrations, mice were neither physiologically nor behaviorally tested prior to enclosure acclimatization), their perception of a nearby predator may increase following extended periods of caudal distraction. In such situations mice may increase their probability of escape at the time of the snake's 1st attempt at capture. Behavioral modification in response to increased awareness of predation risk has been demonstrated in other rodent species (Lima and Dill 1990). Subtle differences in response to snake presence by captive-bred and wild-caught mice (Dell'omo and Alleva 1994) suggest that caudal distraction would be of similar effect on small rodents in natural settings.

When performing caudal distraction, no subject ever positioned its tail close (<30 cm) to its head. Had mice been lured to the tail movement, they would not have been enticed to within striking distance of the snake. Thus, the described behavior appears to serve more as a distraction than it does as a lure to potential prey. Eckert and Karalus (1974) reported that mice may be distracted by auditory stimuli emitted by foraging owls immediately prior to their capture, suggesting that the use and effectiveness of distractive stimuli is a phenomenon worthy of further study.

In answer to the 2nd concern, gray rat snakes often responded to unfamiliar objects or a handler by rapidly vibrating their tails against the substrate, attempting to conceal themselves under leaf litter, or elevating their heads in a strike posture (all recognized defensive behaviors; Greene 1988). The duration of caudal distraction display did not differ between feeding episodes involving the same subject, as might be expected if the behavior were a response to recent handling or an unfamiliar object (in which case shorter durations would occur in successive episodes). The described behavior occurred only in moments before snakes attempted prey capture and was never displayed by subjects foraging for other prey types (e.g., avian prey) in similar enclosure conditions (Mullin 1998). These results collectively suggest that caudal distraction is elicited by visual and/or chemosensory cues that are specific not only to prey type but also to the setting in which the prey is encountered.

Observations described herein indicate that caudal distraction is a unique behavior facilitating capture of small mammals by snakes. However, an alternative explanation for the described tail movement may be that of conflict-induced displacement behavior (Krebs and Davies 1987). Such a view hinges on the assertion that predator approach toward prey is temporarily opposed by the need to remain cryptic so as to avoid detection by, and potential escape of, the prey. Rat snakes initiated caudal distraction more often when advancing toward the mouse than when stationary, however, indicating that any importance associated with crypsis or stealth that might elicit a displacement behavior was negligible. It is also worth noting that caudal distraction was repeatedly displayed by snakes maintained in captivity for durations of 1–16 months, indicating that behavior was not suppressed by conditions of captivity (Warwick 1990).

A few other cautions warrant consideration: *M. domesticus* is not native to the geographic distribution of *Elaphe;* other small rodent taxa sympatric with gray rat snakes (e.g., *Peromyscus, Microtus, Sigmodon,* etc.) may behave differently in response to caudal distraction by snakes during a predator-prey encounter. Edge effects (a feature of noncircular enclosures; Krebs 1989) or space limitations of the enclosure may have masked a difference in ability to capture prey that was dependent upon caudal distraction frequency or duration.

The following observations suggest that much remains to be examined in the functional and ontogenetic development of, as well as the importance of specific stimuli in eliciting, caudal behaviors in *Elaphe.* (1) Whereas caudal luring has been documented in both juveniles and adults of several taxa (Chiszar et al. 1990, Sisk and Jackson 1997, Tiebout 1997, and references therein), caudal distraction has not been observed in rat snakes <2.4 yr old (Mullin 1998). (2) Two adult gray rat snakes were observed performing caudal luring, although without the tail in typical proximity to the head (Carpenter et al. 1978, Jackson and Martin 1980, Tiebout 1997). (3) Luring in gray rat snakes was recorded when foraging for mammalian and avian prey, and in both cases was elicited in response to prey movement. Differences in behavior patterns resulting from the discrimination of prey types have been demonstrated in other taxa (Arnold 1986, Ford and Burghardt 1993) and indicate an appropriate direction for further study of the described behavior. In particular, documentation of the differential display of caudal distraction in snakes exposed to different stimuli may provide evidence for consciousness or awareness to support the few cognitive ethology studies conducted with squamates (Burghardt 1991).

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BLUE GROUSE NESTING PARAMETERS AND HABITAT ASSOCIATIONS IN NORTHEASTERN OREGON

Eric C. Pelren[1] and John A. Crawford[2]

ABSTRACT.—We examined Blue Grouse (*Dendragapus obscurus*) nesting characteristics in northeastern Oregon to identify relationships between hen age and nesting parameters and to ascertain habitat characteristics related to successful nests. Adult and yearling hens exhibited no differences in clutch size, percentage of eggs hatched, nesting success, or hatch dates. Among nests located under logs, 100% (n = 10) hatched ≥1 egg, whereas 58% (n = 10) of 17 nests not under logs hatched ≥1 egg.

Key words: Dendragapus obscurus, *Blue Grouse, nest, age, Oregon, habitat, woody debris.*

Blue Grouse (*Dendragapus obscurus*) occur in a broad range of climatic conditions in western North America. Breeding habitat for this species ranges from mesic conditions in northwestern coastal rain forests to some of the more xeric montane habitats in North America (Zwickel 1992). Nesting parameters of Sooty Blue Grouse (*D. o. fuliginosus*) were extensively examined in coastal British Columbia (Zwickel 1975, Zwickel et al. 1987). Clutch size was greater for adults than for yearlings; no differences in nesting success were reported between these groups. Zwickel and Lance (1965) documented Blue Grouse renesting following nest destruction during late incubation, and Sopuck and Zwickel (1982) noted greater renesting success among adults than among yearlings in British Columbia. Zwickel and Carveth (1978) suggested that hens that laid relatively few eggs deserted nests at a higher rate than other hens.

Nesting parameters have been examined less thoroughly among subspecies of Blue Grouse that occur in interior, more xeric conditions. Caswell (1954) reviewed Blue Grouse nesting parameters and quantified nesting characteristics in Idaho, and Mussehl (1960) estimated hatch dates based on juvenile plumage in Montana; however, no studies related nesting success to hen age or nest habitat.

Our goals were to describe Oregon Blue Grouse (*D. o. pallidus*) nesting characteristics in northeastern Oregon and identify factors that may influence nesting success. Objectives were to identify relationships of hen age with number of eggs/nest, percentage of eggs hatched/nest, nesting success (percent of nests that hatched ≥1 egg), and hatch date; and to examine relationships of nesting success with hatch date and habitat.

STUDY AREA

The study area is on Miller Ridge in the Wallowa-Whitman National Forest, ca 30 km north of Enterprise, Wallowa County, Oregon (Fig. 1). Blue Grouse were captured on a 10-km^2 area of Miller Ridge where elevation ranges from ca 950 to 1500 m.

North-facing slopes here historically were characterized by ponderosa pine (*Pinus ponderosa*) parklands, but land management practices during the last century resulted in encroachment of Douglas-fir (*Pseudotsuga menziesii*) and increased stand densities. Western larch (*Larix occidentalis*) is present, and lodgepole pine (*Pinus contorta*), true firs (*Abies* spp.), and junipers (*Juniperus* spp.) occur at low densities. Drainages contain mixed conifers; aspen and poplars (*Populus* spp.) are rare. Understory and transition-zone shrubs include hawthorn (*Crataegus* spp.), western snowberry (*Symphoricarpos albus*), and mallow ninebark (*Physocarpus malvaceus*). South-slope bunchgrass meadows are dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*). Even- and uneven-aged management was used to harvest timber

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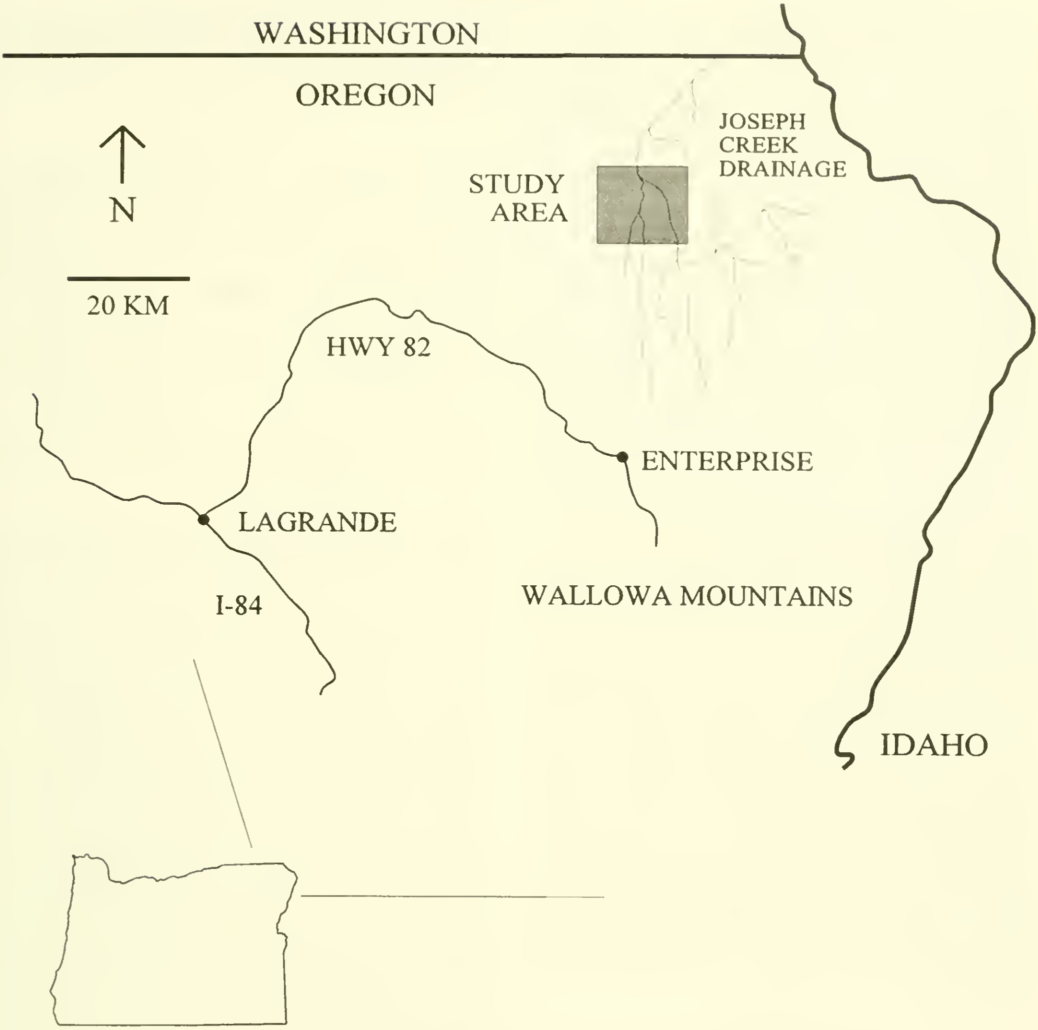

Fig. 1. Blue Grouse nesting ecology study area, Wallowa County, Oregon, 1991–1997.

on the area before and during the study (U.S. Department of Agriculture 1994). Fires periodically burn portions of the area, the most recent occurring in 1986.

Potential predators are abundant on the area. Avian predators include Golden Eagles (*Aquila chrysaetos*), Bald Eagles (*Haliaeetus leucocephalus*), Red-tailed Hawks (*Buteo jamaicensis*), Cooper's Hawks (*Accipiter cooperii*), Northern Goshawks (*Accipiter gentilis*), Great Horned Owls (*Bubo virginianus*), and corvids (*Corvus* spp.). Mammalian predators include badgers (*Taxidea taxus*), black bears (*Ursus americana*), cougars (*Felis concolor*), coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*), ground squirrels (*Spermophilus* spp.), and long-tailed weasels (*Mustela frenata*), all of which are potential nest predators.

Regional topographic and elevational factors contribute to highly variable precipitation and temperature (Johnson and Simon 1987). Precipitation averages 20 cm at 950 m elevation and increases approximately 12.5 cm/300 m increase in elevation (Johnson and Simon 1987). Spring (March through May) precipitation averages 11 cm, and mean minimum temperature is –1°C.

METHODS

Capture and Instrumentation

We captured Blue Grouse and equipped them with radio transmitters following incubation from June through August 1991–1996. Capture devices included interception-style walk-in traps (Pelren and Crawford 1995) and noose poles (Zwickel and Bendell 1967); handling procedures followed established guidelines (Oring et al. 1988). Birds were weighed to the nearest 10 g with Pesola spring scales. We assigned sex by visual examination of wing plumage (Braun 1971, Hoffman 1985). Age was recorded as juvenile or adult, with yearlings classified as adults; each juvenile was reclassified as a yearling at onset of spring following capture and, if monitored for ≥2 yr, as an adult thereafter. A numbered aluminum band was attached to 1 leg. We placed battery-operated 150–151 MHz transmitters weighing approximately 15 g (Advanced Telemetry Systems, Inc., Isanti, MN) or 18 g (Telemetry Systems, Inc., Mequon, WI) on captured females with necklace (Markström et al. 1989) or poncho mounts (Armstrup 1980) modified by a vertical slit at the base of the poncho to prevent esophageal obstruction (Pekins 1988). Transmitters had life expectancies of 12–20 months and were equipped with motion sensors. Juvenile birds with masses <500 g, which represents approximately 50% of adult weight (Boag 1965), were not equipped with transmitters.

Data Collection

Radio-equipped females were located weekly in spring by approach and visual observation to ascertain survival and presence of nests. Nest locations and numbers of eggs were recorded. Grouse on nests were monitored daily by triangulation and detection of radio motion-sensor activation to ascertain dates of departure from nests. We examined nests immediately after hens departed to determine number of eggs, number hatched, and site habitat characteristics. Distance to water and distance to nearest tree >10 cm dbh were noted. Cover type within a 1-m-diameter circular plot centered on the nest was categorized as shrub or grass/forb based on the type that composed the majority of cover. We noted maximum vegetation height within the plot, as well as percent of nest visible from 1 m overhead and average visibility from the 4 cardinal directions at a distance of 1.5 m and height of 1 m. Nests with overhead cover including logs ≥10 cm dbh were noted.

Data Analysis

We used number of eggs/nest, percent of eggs hatched/successful nest, and hatch date as response variables in general linear models (SAS Institute Inc., Cary, NC) to ascertain differences in nesting parameters between adult and yearling hens (indicator variable). To ascertain differences in nesting success between adult and yearling hens, we included hen age as an indicator variable in a logistic regression model with nesting success as a binary response variable. Nests that hatched ≥1 egg were considered successful. We also used a logistic regression model to identify the relationship between hatch date (indicator variable) and nesting success (binary response). One bird was censored from all analyses due to uncertainty concerning hatch date or clutch size, 6 birds with unknown incubation periods were not included in hatch date analyses, and 3 birds of unknown age were excluded from analyses that compared adults and yearlings.

Nest site habitat variables and their interactions were included as indicator variables in a logistic regression model with nesting success as a binary response variable. We used a stepwise selection procedure to identify habitat variables related to nesting success. A multiple regression model was constructed to further examine relationships between reproductive success and nesting habitat. This model included habitat parameters as indicator variables and numbers of eggs hatched as the response variable. All statistical relationships were tested at $P \leq 0.10$ level of significance.

RESULTS

Twenty-seven Blue Grouse hens, monitored from spring 1992 through spring 1997, laid 7.7 ± 0.3 eggs/nest ($\bar{x} \pm s_{\bar{x}}$; Table 1). Among successful nests, 92.0 ± 2.2% of eggs hatched ($\bar{x} \pm s_{\bar{x}}$). Overall nesting success was 74.1 ± 9.0% ($\bar{x} \pm s_{\bar{x}}$). Mean hatch date was 31 May ($s_{\bar{x}} = 2$ d). Adult and yearling hens exhibited no differences in mean numbers of eggs/nest, percent of eggs hatched/successful nest, nesting success, or hatch date. Our observed clutch sizes were larger than noted for Oregon Blue

TABLE 1. Blue Grouse nesting parameters, Wallowa County, Oregon, 1992–1997.

Nesting parameter	Yearlings	Adults	Unknown age	Total
Number of nests	6	18	3	27
Mean hatch date	2 June	29 May	5 June	31 May
% nesting success				
With overhead log	100	100	—	100
Without overhead log	75.0	60.0	33.3	58.8
Total	83.3	77.8	33.3	74.1
All nests				
Total # eggs	46	138	25	209
Total % hatched	78.2	72.5	32.0	68.9
Mean clutch size	7.7	7.7	8.3	7.7
Successful nests				
Total # eggs	39	112	8	159
Total % hatched	91.8	91.3	100	91.8
Mean clutch size	7.8	7.9	8	7.9

Grouse in north central Washington and western Montana (F.C. Zwickel personal communication; Fig. 2) and represent the largest mean clutch sizes for any Blue Grouse populations for which such data exist (Zwickel personal communication).

No relationships were noted between nesting success and hatch date or habitat parameters in the logistic regression models; however, 10 nests under logs were 100% successful, whereas only 10 of 17 nests (58.8%) not under logs were successful. This relationship was not detectable by the logistic regression model because of separation of means among categories. Presence of overhead logs also was related to number of eggs hatched/nest ($R^2 = 0.27$, $P < 0.01$). No other habitat features were related to nesting success or number of eggs hatched per nest.

DISCUSSION

Blue Grouse hens at Miller Ridge exhibited relatively high nesting success (74.1%) compared with populations documented by Zwickel (1992) from British Columbia, Alberta, Washington, Colorado, and Montana (48–81%). At least 1 of 7 unsuccessful nests was trampled by cattle and subsequently predated. The remaining 6 nests were unsuccessful at least partially due to predation. The Miller Ridge population also exhibited higher clutch sizes than observed for other interior populations (Fig. 2). Understanding reasons for these results may aid in management decisions for interior populations.

Although no significant differences were detected in nesting parameters between adult and yearling hens, our sample size was small and may not have been sufficient to detect a difference in mean hatch dates. Observation of earlier hatch dates by adults than by yearlings also was documented by Zwickel (1977) and Hannon et al. (1982). Later nesting by yearlings could serve multiple functions. Yearling Blue Grouse hens typically have smaller mass than adult hens in spring (Zwickel 1992) and may require more time than adults to gain sufficient energy supplies for egg laying and incubation. Also, yearlings must undergo potentially

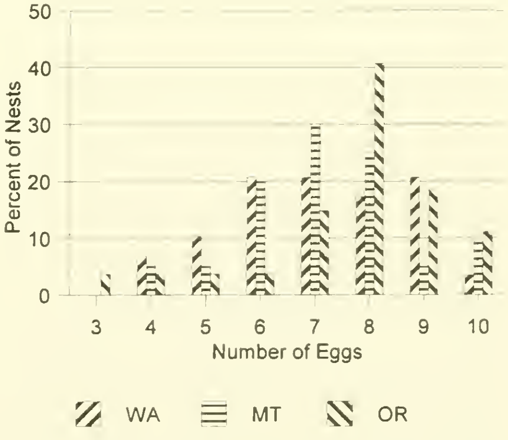

Fig. 2. Percent of nests by size of clutch for Blue Grouse in north central Washington ($n = 29$), western Montana ($n = 20$), and northeastern Oregon ($n = 27$). Washington and Montana data from F.C. Zwickel.

time-consuming searches for nesting territories, whereas adults on our area exhibited philopatry for ranges established during previous years (Pelren 1996). Hannon et al. (1979, 1982) found that reproductive organs develop more slowly in yearling females than in adults and suggested this delay could be a function of social inhibition of yearlings by adult females. Finally, although later nesting carries the disadvantage of lower probability of renesting in the event that the 1st nesting attempt fails, later primary nesting attempts allow time for vegetation and invertebrate food abundance to increase, which may increase nesting or brood-rearing success.

Zwickel (1992) noted that Blue Grouse nest successfully in a wide array of habitat conditions, ranging from nearly bare ground with almost no overhead cover to dense vegetation beneath full forest canopies. Grouse nests at Miller Ridge conformed to this observation. Although Blue Grouse apparently exhibit high tolerance for a variety of nesting conditions, presence of logs may be a common factor in nesting habitat associations among populations. F.C. Zwickel (personal communication) synthesized observations of nesting habitat from interior forests in Alberta, Colorado, Idaho, and Montana and from shrub-steppe habitats in Idaho, Montana, Nevada, Utah, and Washington. Among 61 nests in forest habitats, 13% were under logs; but among 61 nests in shrub-steppe habitat, only 2% were under logs, likely a function of low log availability in this habitat. Shrubs were the primary overhead cover at most nests in both habitats. Zwickel (personal communication) additionally noted that among 450 Blue Grouse nests in early coastal forest seral stages, frequency of use of logs, stumps, snags, or slash as overhead cover increased from 0% in very dense habitat to 47% in very open habitat. Among 605 nests throughout Blue Grouse range, <1% had no overhead cover (Zwickel 1992). Logs may be an important nesting resource in interior forests where vegetation density usually is open compared with coastal habitats. Our observation of 100% nesting success among hens that nested under logs provides inference that, although logs are not an obligate component of nesting habitat, their presence significantly improves chances for successful hatching.

The nests that occurred in association with logs in our study were, in all instances, completely or partially beneath logs that were suspended above the ground by branches or intact root systems. Distance from top of nest cup to bottom of log was approximately 15–50 cm, and many logs were partially burnt from forest fires. Nests also were associated with snags, stumps, branches, and other woody debris, which almost surely contribute to nest concealment; however, presence of overhead cover may be of primary value to nest success.

Blue Grouse in northeastern Oregon frequently nest in parkland habitats. These parkland conditions have decreased on the study area during the past several decades (Pelren 1996). Fire suppression has resulted in encroachment of dense, young stands of Douglas-fir into parkland ponderosa pine habitats, and fuel buildups have resulted in fires that destroyed entire forest stands and woody debris on forest floors, where relatively cool fires historically maintained parkland conditions. Additionally, timber harvest frequently occurred in the form of clearcuts and highgrading during the early 1900s. Recent management, including prescribed fire and timber-extraction techniques that involve thinning and retention of woody debris, may be restoring habitats to conditions similar to those that occurred historically. Our results suggest that management for Blue Grouse should emphasize the return of upland forested habitats to historical parkland conditions, with logs and woody debris present for nesting sites.

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HIGH FOAL MORTALITY LIMITS GROWTH OF A DESERT FERAL HORSE POPULATION IN NEVADA

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ABSTRACT.—A population of feral horses (*Equus caballus*) in the southern Great Basin Desert of Nevada was monitored from 1989 to 1998 to determine size, distribution, and population trends. All individual horses observed in the population were identified by unique markings during the first 2 yr of study, and most animals could be observed annually. During this study no new horses were identified in the population, indicating that no immigration occurred from outside populations. The population reached a high of 65 horses yearling or older in 1992 and declined each year thereafter, reaching a low of 36 horses in 1998. Estimated foal survival averaged <12% over 8 yr. Only 11 horses were recruited into the population as yearlings or older animals during the study. Mountain lion predation is hypothesized as a major factor limiting growth of this feral horse population.

Key words: feral horse, Equus caballus, *foal survival, finite rate of increase, southern Nevada, Great Basin Desert.*

During the past 2 decades or more, populations of feral horses (*Equus caballus*) have shown dramatic increases at many locations in western United States, necessitating costly removal and adoption programs (Eagle et al. 1992, Garrott et al. 1992). A small herd of feral horses was known to persist at the Nevada Test Site (NTS) prior to its inception as a nuclear weapons testing facility in 1951, although a census was never performed. The U.S. Department of Energy (DOE) initiated a long-term horse monitoring program at NTS in 1989. This study was initiated to monitor potential increases in the horse population and evaluate the need for control (i.e., removals). In this paper we report findings of distribution, abundance, band structure, sex ratio, foal survival, and population growth rate of the NTS feral horse population from 1989 to 1998.

STUDY AREA

NTS, a large (3500-km^2) facility operated by DOE, is approximately 100 km northwest of Las Vegas, Nevada, and was used primarily for nuclear weapons testing from 1951 through 1992. All nuclear weapons tests conducted at NTS were underground beginning in July 1962. Most cattle and other livestock were removed from NTS prior to commencement of testing in January 1951; thereafter, impacts from grazing were limited to an experimental cow herd and some feral horses (DOE 1992).

Horses occur only in the northern 1/3 of NTS (Fig. 1). Vegetation of this region is dominated by big sagebrush (*Artemisia tridentata*) or black sagebrush (*A. nova*), pinyon pine (*Pinus monophyla*), and Utah juniper (*Juniperus osteosperma*) at higher elevations, with desert shrubs, primarily fourwing saltbush, (*Atriplex canescens*), blackbrush (*Coleogyne ramosissima*), Nevada jointfir (*Ephedra nevadensis*), white burrobrush (*Hymenoclea salsola*), and Anderson's wolfberry (*Lycium andersonii*), at lower elevations. Common grasses in the study area include Indian ricegrass (*Achnatherum hymenoides*), desert needlegrass (*A. speciosa*), purple threeawn (*Aristida purpurea*), foxtail brome (*Bromus rubens*), cheatgrass (*B. tectorum*), and galleta (*Pleuraphis jamesii*). Topographic features of the study region include forested mesas, open and forested ridges, rolling hills, narrow canyons, rock outcrops, washes, open bajadas, and flats. Mean annual rainfall (1965–1997) was 23.2 cm (s = 9.9) recorded at Tippipah Spring weather station (1518 m) near the Eleana Range. Historical mean minimum and maximum air temperatures were –3.4°C and 27°C, respectively, in sagebrush habitat west of Rainier Mesa (Beatley 1976). The northern 2/3 of NTS is in the Great Basin Desert and the southern 1/3

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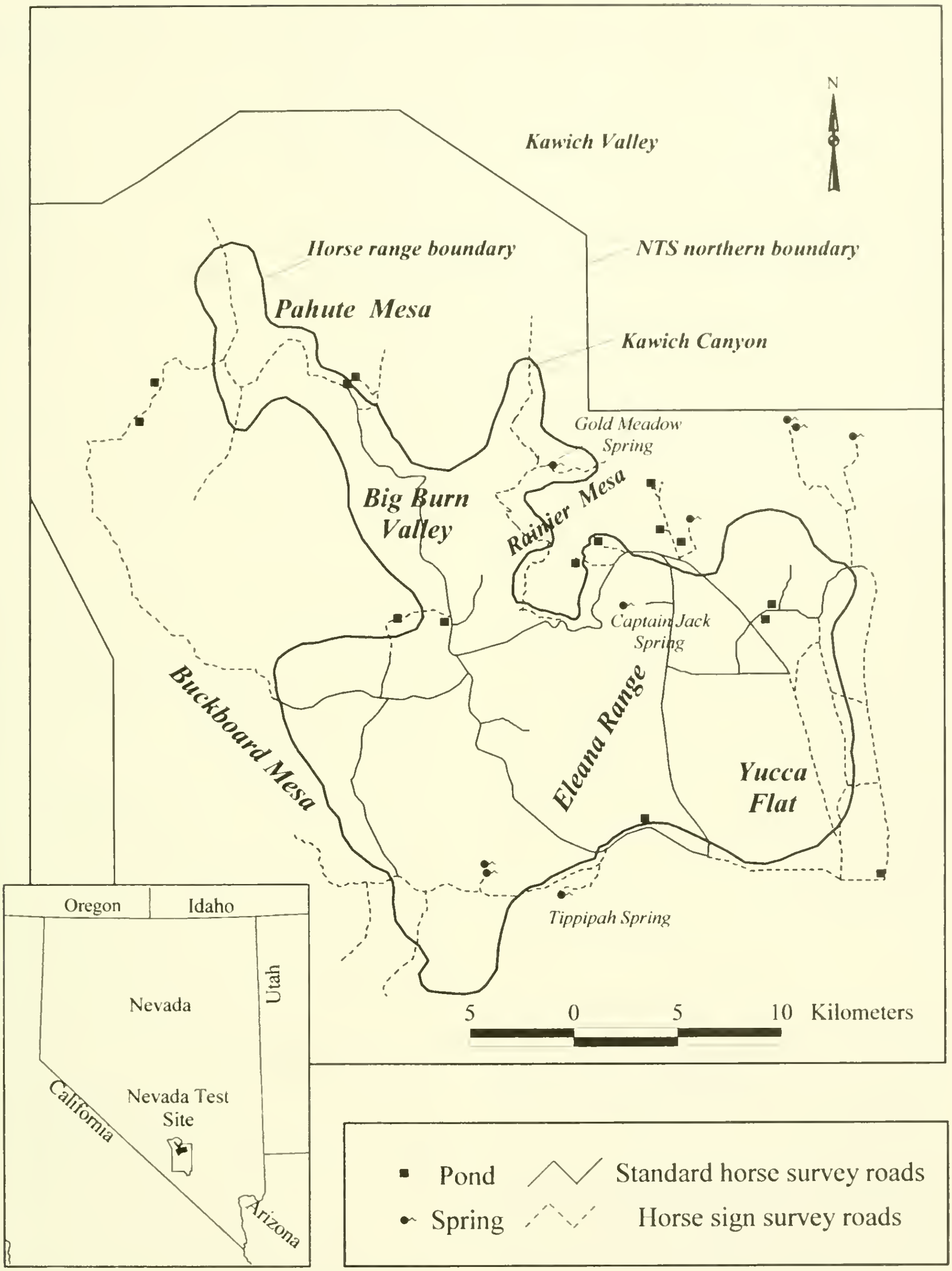
N
Kawich Valley
Horse range boundary
NTS northern boundary
Pahute Mesa
Kawich Canyon
Gold Meadow Spring
Big Burn Valley
Rainier Mesa
Captain Jack Spring
Buckboard Mesa
Eleana Range
Yucca Flat
Tippipah Spring
5 0 5 10 Kilometers
Oregon
Idaho
Nevada
Utah
Nevada Test Site
California
Arizona
Pond
Spring
Standard horse survey roads
Horse sign survey roads

Fig. 1. Perimeter boundary of feral horse distribution on the Nevada Test Site with survey roads, locations of water sources, and major topographic features.

within the Mohave Desert. Details of vegetation, climate, geology, and physiography of the region are found in O'Farrell and Emery (1976) and Beatley (1976).

METHODS

Feral horses occupied habitats between 1250 and ca 2300 m in the Eleana Range and adjacent foothills in the northern 1/3 of NTS in a 450-km^2 region of transition zone between the Mohave and Great Basin deserts (Fig. 1). Horses were common from northern Yucca Flat on the east, to Buckboard Mesa on the west, near Tippipah Spring on the south, to Big Burn Valley, Gold Meadows, and Kawich Canyon on the north. Horses and their sign were also observed on Rainier Mesa (2300 m) and Pahute Mesa (2150 m), but usage was much more common at elevations below 2000 m. Horse use of water sources was determined by recording horse sign and sightings at water sources on NTS from 1987 to 1998. Horse sign was also recorded along specific roads during surveys to approximate the horse range boundary (Fig. 1). These surveys indicated that horses do not maintain populations in any other regions on NTS. Large groups of up to 90 horses from a separate population in Kawich Valley were observed crossing the NTS northern boundary, but they do not reside there permanently.

We attempted to identify and count all horses on NTS each year while driving a standard road route (120-km length) at speeds of 8–60 kph and searching areas distant from roads on foot (Fig. 1). Standard surveys were conducted weekly from March through October 1990–1994 to establish population size and estimate foal survival. During 1995–1998 we conducted surveys from June through October at a frequency similar to that of previous years. Biologists stopped to locate horses with binoculars at specified locations along the route where views were unrestricted and censused areas around water sources. Several natural springs (including Captain Jack Spring and Gold Meadows Spring) and several man-made ponds were used heavily by horses throughout the study (Fig. 1). Horses were easily viewed and identified because horse trails often were adjacent to roads and horses were habituated to humans.

During the 1st year of study (1989–90), most horses were identified and horses of unknown age were subjectively classified as adults. To identify individuals, we photographed horses when they were initially observed and classified them according to body color (e.g., bay, black), unique facial markings, and sock and stocking patterns (Berger 1986, Pacheco and Herrera 1997). Once horses were located from vehicles, biologists approached the animals on foot to within 100 m to identify individuals and note sex, presence or absence of foals, band size, and harem size. Bands were defined as a group of ≥1 males and females, ≥1 yr old, living together for ≥3 months duration. Harem size included all female horses in a band that were ≥1 yr old excluding daughters (i.e., females born and living within their natal band), living together for ≥3 months. Horses not observed during 1 yr but seen in the next were counted as present the previous year.

Foaling rates (1990–1994) were determined by dividing the number of females present (≥3 yr old) into number of foals observed that year. Maximum foal survival for 1990–1994 was estimated by dividing the number of foals seen during their year of birth into the number alive the following year.

A log-linear regression of horse count data (≥1 yr old) across years was conducted. Following Eberhardt (1987), the slope of the regression line from a series of log-transformed counts estimates the instantaneous annual rate of increase (r), and the antilog of r estimates the mean rate of change (λ). A population that is increasing over time has values of $\lambda > 1.0$, whereas a population exhibiting no change in size has $\lambda = 1.0$. A population that is decreasing in size over time has $\lambda < 1.0$.

Kruskal-Wallis tests were used to test for changes in band and harem size across years. A chi-square test was used to examine changes in horse sex ratios across years.

RESULTS

The number of horse bands present decreased from a maximum of 14 in 1990 to a minimum of 8 in 1998. Mean band size of horses (excluding foals) varied from a maximum of 4.3 in 1992 to a minimum of 3.4 in 1997 ($\bar{x} = 3.8$, $s = 1.5$) and did not change significantly across years ($H = 2.74$, 8 df, $P = 0.95$). Mean harem size (excluding daughters)

TABLE 1. Number of feral horses counted at the Nevada Test Site during March–October 1990–1994 and June–October 1995–1998. Foals were counted only from 1990 to 1994.

Number of surveys	43	41	43	30	32	20	14	22	16
	Year								
Age class	1990	1991	1992	1993	1994	1995	1996	1997	1998
Adults	59	57	57	57	53	51	45	39	36
3-yr-olds	—	—	2	2	3	0	0	1	0
2-yr-olds	—	2	2	4	0	0	1	0	0
Yearlings	2	2	4	0	0	3	0	0	0
Total (≥1 yr old)	61	61	65	63	56	54	46	40	36
Foals	9	12	17	11	11	—	—	—	—

varied from a maximum of 2.7 in 1992 to a minimum of 2.3 in 1997 ($\bar{x}$ = 2.4, s = 1.5) and did not change significantly across years (H = 0.62, 8 df, P = 0.99). The male-to-female sex ratio (≥2 yr old) averaged 0.78:1.0 over 9 yr and did not change significantly during the study (χ^2 = 0.58, 8 df, P = 0.99).

Most individuals in the population could be counted in ≤20 surveys, although in most years >20 surveys were conducted (Table 1). For example, during 1990, 56 of 61 horses known to be alive (92%) were observed after 20 surveys, and from 1991 to 1995 only 1 additional horse was identified from the population after 16 surveys had been conducted.

The log regression of horse count across years (Fig. 2) was significant (R^2 = 0.83, 8 df, P = 0.0007). Number of horses ≥1 yr old decreased from a high of 65 in 1992 to 36 in 1998 (Table 1), a decline of 45%. Exponential rate of change (r) estimated for the horse population (≥1 yr old) from 1990 to 1998 was –0.07, and finite rate of change (λ) was 0.93 (±95%, CI = 0.91–0.96). Only 11 horses were recruited to the population (yearlings or older) from 1990 to 1998, and only 7 of these survived to adult age or older.

Numbers of foals observed annually ranged from 9 to 17 between 1990 and 1994 (Table 1). Mean estimated foaling rate for females (≥3 yr old), 1990–1994, was 36% and varied from 26% to 50%. Fifty-two foals observed were missing and only 2 were found dead between 1990 and 1994. Most foals were born from late March through July and were missing between late April and August. Foal counts were not reported from 1995 to 1997 because horse sampling began in June during those years. However, no yearlings were observed between 1996 and 1998, indicating that any foals born did not survive to the end of the following year. Therefore, estimated maximal foal survival to yearling age was 22, 33, 0, 0, 27, 0, 0, 0%, respectively, 1990–1997 (12% average). Actual foal survival was probably lower because all foals born were not observed (i.e., some mares visually classified as pregnant were not observed with foals).

No horses immigrated into this population from 1991 through 1998. All horses were identified by 1990 or were first seen as foals or yearlings. Only 4 fresh carcasses of 34 missing or dead horses (excluding foals) were located during 9 yr. Five horses (≥1 yr old) were missing or dead from 1990 to 1993. Twenty-nine horses (≥1 yr old) were missing or dead 1994–1998. Once a horse was missing, it was rarely seen again. In only 2 cases during 8 yr was a horse not seen in a year and observed again in later years.

DISCUSSION

Total absence of new horses observed in the NTS population suggests that immigration from large horse populations north of NTS did not occur during this study. Emigration, although unlikely, cannot be discounted as an explanation for disappearance of 30 horses ≥1 yr old during this study. Some missing horses could have emigrated to populations 20–30 km north and west of NTS, but lack of water sources (for >20 km) in those directions and structural barriers to the north (rugged forested terrain and playas) that restrict movements (Berger 1986) make this unlikely.

Mean rate of change (λ) for this population (0.93) was much lower than rates reported from all other feral horse populations in western United States, including the Granite Range

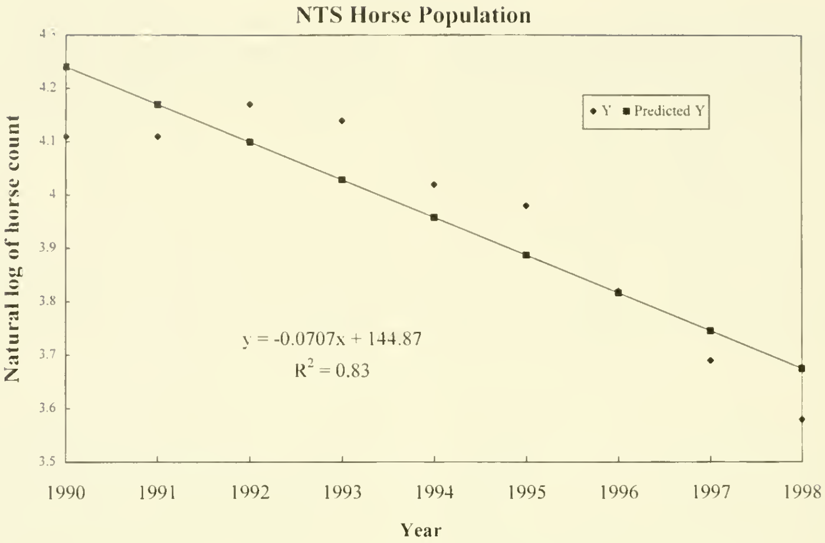

Fig. 2. Log-linear regression of horse count versus year at the Nevada Test Site, 1990–1998.

in Nevada (1.18; Berger 1986) and other populations in Nevada (1.08–1.27; Garrott et al. 1991, Wolfe 1980), the Pryor Mountains of Montana (1.18; Garrott and Taylor 1990), Wyoming (1.14–1.26; Garrott et al. 1991, Wolfe 1980), Idaho (1.15; Garrott et al. 1991), and Oregon (1.16–1.27; Eberhardt et al. 1982, Garrott et al. 1991). Each year healthy, unweaned foals were missing from bands within 6 months after they were first observed, indicating that they did not survive. Foal survival measured on NTS (<12%) was much lower than most other studies (67–93%) from North America (Keiper and Houpt 1984, Berger 1986, Siniff et al. 1986, Wolfe 1986, Garrott and Taylor 1990) and appears to be the major factor limiting growth of this population. Only Turner et al. (1991) reported foal survival of 27%, comparable to our results.

Mean foaling rate (0.36) for NTS was lower than foaling rates reported elsewhere in the western U.S. (range 0.37–0.71; Kirkpatrick and Turner 1986, Berger 1986, respectively), although this rate was probably underestimated because some foals were undetected each year.

During each year of study, mountain lions or their sign (tracks, scats, or deer kills) were observed within the NTS horse range. While causes of foal mortality were not studied, we hypothesize that 1 factor limiting growth of the NTS horse population may be mountain lion predation. This hypothesis is supported by the consistent yearly disappearance of healthy unweaned foals and by some direct evidence of mountain lion predation. These include 2 mountain lion kills (1 foal and an adult horse) and 3 injured foals (with apparent mountain lion bite marks or wounds on the neck and hind quarters), resulting in death or missing animals. Our observations are consistent with those of Turner et al. (1991), who found that drag marks, tracks, partially buried remains, and canine tooth punctures on defleshed head and legs were strong evidence for cause of death by lions. Turner et al. (1991) also reported that mountain lion predation caused poor foal survival, and change in the horse population was limited to 4–8% over 5 yr in Montgomery Pass Wild Horse Territory on the Nevada–California border.

Horses are restricted to higher-elevation habitats (>1600 m) May–October on NTS, coinciding with the period when most foals disappear. These habitats, heavily forested with pinyon-juniper, have rugged terrain and numerous canyons, and horses may be at higher risk to mountain lion predation here than in other more open habitats (large, unforested, flat valleys) at lower elevations.

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NEGATIVE EFFECTS OF THE WESTERN THATCHING ANT (*FORMICA OBSCURIPES*) ON SPIDERS (ARANEAE) INHABITING BIG SAGEBRUSH (*ARTEMISIA TRIDENTATA*)

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ABSTRACT.—The effect of thatching ants (*Formica obscuripes*) on number of spiders found on sagebrush (*Artemisia tridentata*) was determined by comparing spider abundance on shrubs at different distances from ant mounds. Spider abundance was inversely related to proximity to mounds. Spider abundance on shrubs around abandoned mounds revealed no effects of mound proximity. Two mounds in which ants were exterminated showed a declining effect of mound proximity 1 month after treatment. One year after treatment there was no effect.

Key words: Araneae, Formica obscuripes, Artemisia tridentata, *competition.*

Ants exert significant influences on their environments (Petal 1978) by limiting plant growth (Ryti 1992) or increasing heterogeneity of plant communities (Beattie and Culver 1977). "In the forests of Finland ants are the premier predators, scavengers, and turners of soil" (Hölldobler and Wilson 1994:6). Many ants significantly reduce populations of arthropods within their foraging area because of their intensive foraging activity, social life, and polyphagy (Petal 1978, Hölldobler and Wilson 1990, McIver et al. 1997).

Thatching ants (*Formica obscuripes*) produce large mounds that are covered by small pieces of plant material, often at the base of a shrub (Allred 1982). They prey on insects, forage on dead insects, consume honeydew which they harvest from aphids, and occasionally eat plant tissue (Wheeler and Wheeler 1963, Beattie and Culver 1977, Petal 1978, Douglas and Sudd 1980, Hölldobler and Wilson 1994).

No significant differences were found in the spider fauna of areas inside and outside the hunting area of the red wood ant, *Formica polyctena* (Brüning 1991), and spider species composition was not influenced by presence of ant mounds in the Netherlands (Van der Aart and DeWit 1971). Yet, an experimental removal of ants from canopies of Douglas-fir (*Pseudotsuga menziesii*) increased the number of hunting spiders (Halaj et al. 1997).

Casual observations of spider abundance on shrubs at varying distances from mounds of *F. obscuripes* suggested that ants depress spider abundances. In this study the effect of *F. obscuripes* on spider abundance on sagebrush was measured at varying distances from active ant mounds, abandoned mounds, and mounds from which ants were exterminated.

METHODS

Surveys were conducted at 2 sites in the Cache National Forest, Cache County, Utah: High Creek, which is northeast of Richmond at 41°55′55″N, 111°46′20″W, and Cherry Creek, 4.8 km south of High Creek at 41°58′43″N, 111°44′44″W. Both are in shrub-steppe habitat at 1600 m elevation.

Three treatments were studied: active ant mounds, abandoned ant mounds, and mounds in which ants were removed by treating with 225 g granular Diazanon per mound watered in with 2 gallons of water.

Surveys of spiders on sagebrush near 2 active ant mounds at High Creek were conducted in June and August 1995 and August 1996. Spiders on sagebrush near 4 active mounds at Cherry Creek were surveyed in August 1996. Surveys of spiders on sagebrush near 3 abandoned ant mounds at Cherry Creek were conducted during August 1996. Ants were experimentally eliminated from 2 mounds at Cherry Creek in August 1997, and the subsequent effect on spider abundance was measured in September 1997 and July 1998.

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TABLE 1. Variables associated with each thatching ant mound and results of the regression of distance from mound and spider abundance (transformed to square root of spider abundance).

Year	Treatment	Date	Mound	*P*	Y- intercept	Slope
1995	Active	30 June	HC1[a]	0.004	0.7	0.195
	Active	13 Aug	HC2	0.048	2.3	0.048
1996	Active	15 Aug	HC1	0.000	1.8	0.488
	Active	15 Aug	HC2	0.000	2.2	0.494
	Active	1 Aug	CC1[b]	0.008	1.5	0.268
	Active	1 Aug	CC2	0.003	0.1	0.305
	Active	6 Aug	CC3	0.004	0.4	0.490
	Active	6 Aug	CC4	0.001	–0.5	0.629
	Abandoned	17 Aug	CCA1	0.303	4.6	0.155
	Abandoned	17 Aug	CCA2	0.289	4.8	0.107
	Abandoned	17 Aug	CCA3	0.491	4.7	–0.130
	Treated	11 Sept	CC 2	0.014	2.4	0.154
	Treated	11 Sept	CC 3	0.029	2.4	0.160
1997	Treated	24 July	CC 2	0.237	2.5	0.090
	Treated	24 July	CC 3	0.092	2.4	0.111

[a] HC = High Creek.

[b] CC = Cherry Creek.

Surveys were conducted by establishing three 12-m lines from each mound and collecting spiders on each shrub along these lines. The 3 lines were visually selected so they would intersect the greatest number of shrubs and still be relatively evenly spaced around the mound. Spiders were collected using a beating sheet (Southwood 1978), after which they were preserved in 70% ethanol and taken to the laboratory for sorting and counting. The distance from the mound to each shrub was measured to the nearest 0.1 m.

RESULTS

Analysis was conducted for individual mounds because size of mound, size of shrub, and time of year can affect number of spiders found on shrubs. Regression analysis was used to examine the relationship of spider abundance on sagebrush and proximity to thatching ant mounds. Spider numbers were transformed using the square root of spider abundance per shrub to reduce differences in variance. Results are shown in Table 1.

Regression analyses for surveys of spider abundance near the 3 abandoned mounds found no significant relationship between distance of shrubs from the mound and spider abundance per shrub ($P = 0.289–0.491$). Eight regression analyses for surveys of active mounds were significant ($P = 0.001–0.048$); however, it was not logical that the number of spiders would rise continuously. There had to be a point at which the number of spiders would no longer increase as distance from the mound increased.

To identify the distance where the effect of ants was not significant, a series of regression equations was produced for each active mound. In the 1st step the data were divided into 2 groups based on a fixed distance from the mound, and a regression line was fitted to each set of data. This was done repeatedly by regrouping the data at 1-m intervals from 2 to 9 m to find the point that divided the data into 2 groups in which the group closer to the mound had a significant positive slope and the more distant group had a slope that was not significantly different from zero. When a distance was identified, the analysis was refined by repeating the process by dividing the distance into groups based on 0.1-m increments. The distance that met the criteria listed above and had the lowest sum of squared residuals was identified and used in the next procedure.

Once a point was identified, a new single regression equation was computed in which the slope of the regression line was assumed to change at the point identified. Both slopes were then forced through a single point at the identified distance. Results are shown in Table 2.

Identified points ranged from 6.0 to 8.6 m from mounds. Curves produced by this procedure significantly fit the data ($P = 0.001–0.039$). Y-intercepts ranged from – 0.10 to 1.80. Since the data were transformed, the number of spiders at zero distance from the mound ranged from –0.01 to 3.2.

TABLE 2. Parameters derived from 2 slope models developed to predict the effect of proximity to thatching ant mounds on spider abundance on sagebrush.

Year	Mound	D (distance to slope change)	*P* for model	Predicted spider abundance at 0.0 m from mound	Slope for 0.0 to D	Predicted spider abundance where slope changes to zero
1995	HC1[a]	8.0	0.004	0.16	0.28	2.7
	HC2	8.6	0.039	3.24	0.32	4.4
1996	HC1	7.0	0.001	1.04	0.74	6.2
	HC2	7.7	0.002	0.0004	0.55	5.9
	CC1[b]	8.0	0.012	–0.0004	0.62	4.8
	CC2	6.0	0.000	–0.0001	0.61	4.0
	CC3	7.8	0.009	0.25	0.50	4.4
	CC4	8.0	0.002	–0.01	0.36	2.8
	CC2 (treated)	8.1	NS			
	CC3 (treated)	8.0	NS			

[a] HC = High Creek.
[b] CC = Cherry Creek.

Regression analyses of the data from the surveys of spiders on sagebrush around the 2 treated mounds (1 month after treatment) showed a significant effect of distance from mound on spider abundance (Table 1). When the above procedure was used to identify the point at which there was no effect of ants on spiders for treated mounds, either a point could not be identified or the model produced by the procedure was not significant (P = 0.059).

DISCUSSION

The presence of thatching ants on sagebrush near their mounds had a significant, negative effect on abundance of spiders on sagebrush. Negative interactions occurred up to 8.6 m from active mounds. The number of spiders on sagebrush 0.0 m from active mounds was predicted to be close to zero, although the regression equation for 1 mound predicted 3.2 spiders. The number of spiders on sagebrush at distances beyond the effect of ants ranged from 2.7 to 5.9 per shrub.

Spider abundance on sagebrush near mounds which were no longer active was not affected by shrub proximity to the mound. One month after an experimental extermination of 2 mounds, there was still a significant, negative residual effect on spider abundance. However, the effects of ant removal were beginning to show in that the Y-intercept changed from the equivalent of no spiders at 0.0 m from the mound before treatment to 5.8 spiders 1 month after treatment, and significant models to predict the extent of the effect could not be produced. One year after treatment there was no effect of proximity to the mound on spider abundance. It appears that the presence of ants on sagebrush and not proximity of the mound negatively affected spider abundance.

The principal influence of ants on spider abundance may be due to competition (Wise 1993). *Formica* aggressively defend 1 of their primary food sources, aphids, from attack (Bradley 1973, Douglas and Sund 1980, Messina 1981, Ryti 1992, Seibert 1992). The magnitude of spider predation on aphids is variable (Toft 1995, Sunderland et al. 1986); some studies show a significant and others a minimal effect. Ants may not differentiate among arthropods that threaten 1 of their major food sources but may aggressively attack any species that is encountered. While samples collected from Cherry Creek were being sorted, a worker ant was found with a spider in its mandibles.

The relationship between thatching ants and spiders may represent a form of interference competition. Spiders, as generalist predators, will attack aphids when they are encountered, and ants protect their source of honeydew by killing or chasing spiders. Since spiders also eat ants, the aggressive behavior of ants toward spiders eliminates not only a competitor but also a potential predator. Evidence from this study for competitive interference by thatching ants on spiders comes from relationships identified by the regressions described above. Shrub distance from the ant mound was significantly related to number of spiders found on a shrub. Shrubs closer to the mound had fewer spiders. This effect was observed only for shrubs within 6–9 m of the mound.

Additional studies are needed to ascertain whether the effect of ants on spider abundance on sagebrush within 6 m of the mound is due to predation or protection of aphids.

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ANATOMY OF ROCKCRESS PSEUDOFLOWERS CAUSED BY *PUCCINIA CONSIMILIS*

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ABSTRACT.—*Arabis pulchra* plants infected by the crucifer rust fungus (*Puccinia consimilis*) develop pseudoflowers. These pseudoflowers are characterized by stems with short internodes and numerous closely spaced, bright yellow leaves coated with a sweet sugary substance. Pseudoflowers do not resemble normal *A. pulchra* flowers. Pseudoflowers, leaves, and stems of *A. pulchra* plants infected with *P. consimilis* and true flowers, stems, and leaves of uninfected *A. pulchra* plants were fixed, embedded, sectioned, and stained using standard microtechniques. Epidermal, ground, and vascular tissues of true leaves, true petals, and pseudopetals were examined and compared for anatomic differences. Examination of anatomic characteristics revealed that pseudopetals are modified leaves.

Key words: rockcress, Arabis pulchra, *fungus rust,* Puccinia consimilis, *pseudoflowers.*

Arabis species infected with the fungus rust *Puccinia consimilis* develop stems with short internodes and numerous closely spaced, bright yellow leaves. These structures are called pseudoflowers since they are brightly colored, have a sweet sugary substance, attract insect pollinators, but lack plant reproductive structures (Roy 1993). Instead, spermagonia of the fungus are embedded in pseudopetals and the nectarlike substance contains numerous spermatia. For fertilization (initially plasmogamy and, later in the rust life cycle, karyogamy) to occur, the haploid spermatia must be transferred to the receptive hyphae of another mating type. For the rust fungi, this transfer is accomplished by insects. In the *Arabis-Puccinia* interaction, the rust-induced morphological change to attract insect pollinators is more extensive than with other host-rust interactions (Roy 1994). The anatomic basis of this large morphological change was examined. Objectives of this research were to determine whether leaves of pseudoflowers are composed of modified true leaves as suggested by Roy (1993, 1994) or modified true petals. In addition, the extent of the modification at the anatomic level was examined.

MATERIALS AND METHODS

Pseudoflowers, leaves, and stems of *Arabis pulchra* plants infected with *Puccinia consimilis* and true flowers, stems, and leaves of uninfected *A. pulchra* plants were fixed in FAA (65% formaldehyde, 5% acetic acid, 30% ethanol) in the field on 10 March 1996 and 19 April 1997. The collection site is approximately 1 km northeast of the Moab, Utah, landfill. In the lab specimens were aspirated under slight vacuum and then placed in fresh FAA. As needed, subsamples of the specimens were removed, dehydrated in a graded, ethanol-tertiary butyl alcohol series and embedded in Paraplast. Sections 8–12 µm thick were cut on an AO "820" Spencer rotary microtome with a steel blade, mounted on glass slides, and stained with safranin and fast green (Berlyn and Miksche 1976). Hemo-De (Fischer Scientific, Pittsburg, PA) was substituted for xylene in the stain series. Slides were viewed and photographed on an Olympus BH-2 microscope mounted with an Olympus PM-10AK 35-mm camera. Voucher specimens of *A. pulchra* were deposited in the Weber State University Herbarium.

RESULTS

Leaves of healthy *A. pulchra* plants are green and lorate in shape. The adaxial and abaxial epidermises have numerous, multicellular branched trichomes (Fig. 1). The mesophyll tissue is 7–10 layers thick and is not differentiated into distinct palisade and spongy

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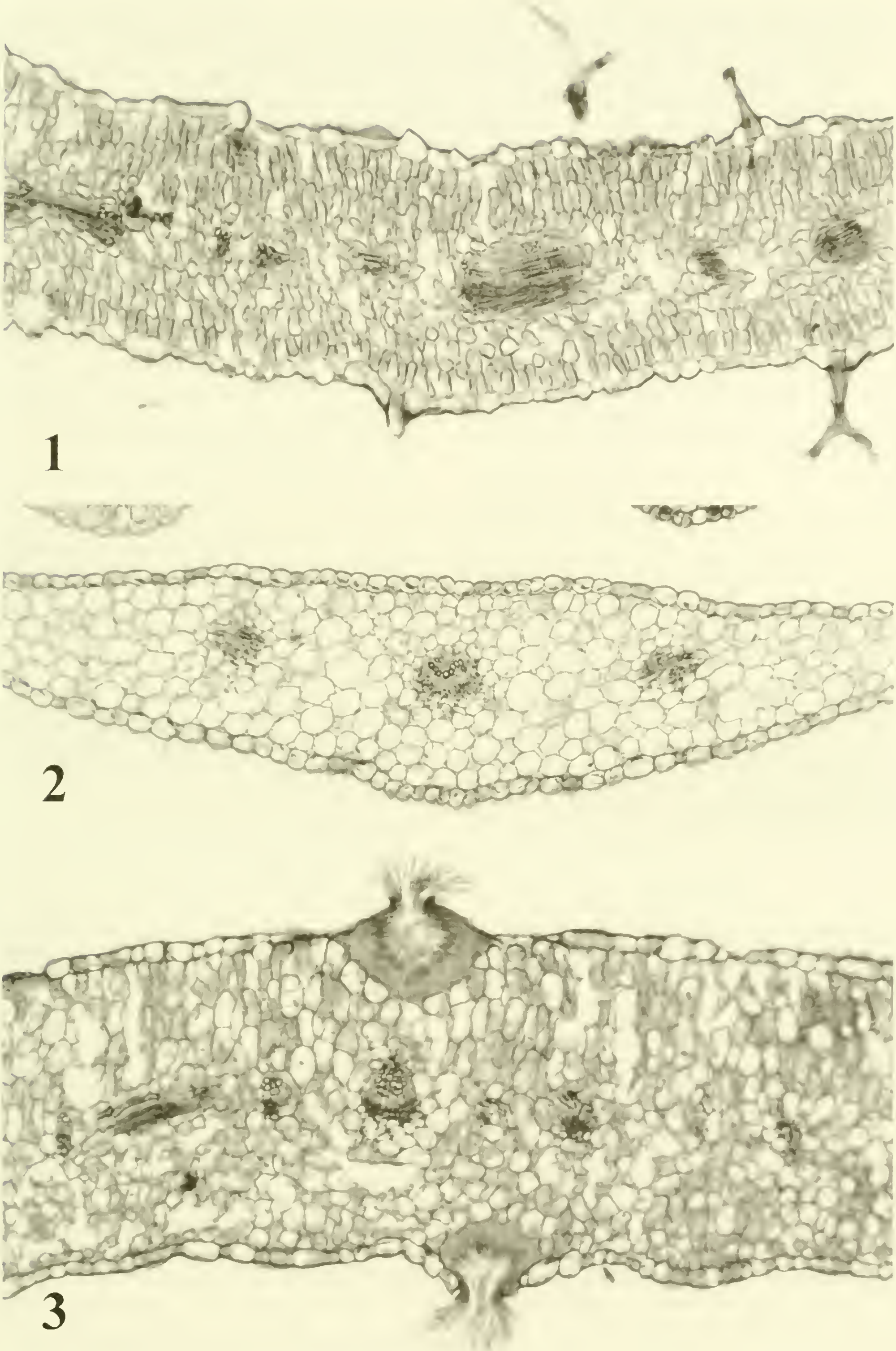

Figs. 1–3. Transverse sections of a healthy *Arabis pulchra* leaf (Fig. 1), true petal (Fig. 2), and pseudopetal showing 2 erumpent spermagonia (Fig. 3).

layers. In general, mesophyll cells are slightly columnar (i.e., 1.5–2 times taller than wide) and have numerous chloroplasts. The midvein is surrounded by rib tissue but lateral veins are generally embedded in mesophyll and lack rib tissue. All vascular bundles are collateral and laterals are surrounded by a single layer, parenchymous bundle sheath (Fig. 1).

True petals of uninfected plants are white to pale violet colored and are ephemeral. Petals lack trichomes and the epidermis is composed of more uniformly shaped cells than the leaf epidermis (Fig. 2). Mesophyll cells are isodiametric and lack chloroplasts. Vascular bundles are collateral, entirely embedded in mesophyll, and are surrounded by a single layer, parenchymous bundle sheath (Fig. 2).

Pseudopetals are yellow colored and spatulate to obovate in shape. Thus, they are shorter and broader than uninfected leaves. Pseudopetals have few to no trichomes. When present on infected plants, branched multicellular trichomes are restricted to areas with few to no spermagonia. The mesophyll tissue is 7–10 layers thick and is not differentiated into distinct palisade and spongy layers (Fig. 3). Mesophyll cells of pseudopetals are generally wider than mesophyll cells of healthy leaves. The midvein is surrounded by rib tissue but lateral veins are generally embedded in mesophyll and lack rib tissue. All vascular bundles are collateral and laterals are surrounded by a single layer, parenchymous bundle sheath (Fig. 3).

DISCUSSION

This study verified what Roy (1993, 1994) suggested. Pseudopetals of *A. pulchra* plants infected with *P. consimilis* are modified leaves. Here I show similarities to leaves based on similarities in ground epidermal cell shape, multicellular trichomes, mesophyll cell shape, number of mesophyll cell layers, and rib tissue surrounding the midvein. Anatomic features of true petals are distinct from both true leaves and pseudopetals. Major effects of *P. consimilis* infection are a change in leaf shape and a decrease in internodal distance. Except for a large reduction in number of trichomes, anatomy is not greatly different between true leaves and pseudopetals. The lack of significant anatomic differences between true leaves and pseudopetals is noteworthy as the rust-induced morphological change to attract the insect pollinators is more extensive than with other host-rust interactions (Roy 1994).

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ADDITIONAL COMMENTS ON THE NESTING BEHAVIOR OF *BATRACHOSEPS WRIGHTI* (BISHOP)

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Key words: nesting, trailways, communal nests, Batrachoseps wrighti.

Since the description of *Plethopsis wrighti* (Bishop 1937) and a report by Stebbins and Lowe (1949) that provided characteristics relating it to the genus *Batrachoseps*, much attention has been focused on reproduction (Stebbins 1949, Tanner 1953, Jockusch and Mahoney 1997). My intent in this paper is to review and provide further explanation of the reproduction and nesting behavior of *B. wrighti*, based on a reexamination of my field notes and observations made in 1952.

The discovery of *B. wrighti* in rotting fir logs was first reported by Bishop (1937). This species was also found in logs by Tanner (1953) and Jockusch and Mahoney (1997); see also Petranka 1998:234. Adults and juveniles also occur under fallen limbs, chips, and other surface objects, suggesting that they forage and disperse through various forest habitats. On several collecting trips in Oregon I have found adults and juveniles abroad and not always near rotting fir logs; these observations include records from Clakamas County, June 1952, 1954 (BYU 10344, 11224–11228); Multnomah County, June 1954 (BYU 12631–12632); Linn County, June 1963 (BYU 31981–31995); and Marion County, May 1985 (BYU 12693). Whether nesting occurs only in rotting logs or whether surface debris mentioned above is used is yet to be determined. Dying trees and fallen logs are attacked by different species of boring beetles that make trailways in wood immediately beneath the bark. Dr. S.L. Wood, an authority on bark beetles, advised me that some of the large Cerambycidae occurring in Oregon are capable of making the large trailways in which salamanders noted above were found. Trailways reported by Tanner (1953) crisscrossed the log, with some pupation tunnels ending in a hole deep within the log. Salamanders were found within the log, although most were in trailways just beneath the bark.

Batrachoseps wrighti eggs, found in an enlargement of a trailway on 19 June 1952, were in a spiral cluster surrounded by soggy wood fibers. The female was nestled in wood fibers on the perimeter of the nest with a few fibers between her and the eggs (Fig. 1). The nesting chamber, although not measured, provided ample room for the female to occupy the nesting area. For further clarification and to avoid a misconception, it is important to note that the attending adult was identified as a female (see Jockusch and Mahoney 1997:703–704). She was not in direct contact with the eggs; nor did it appear, from my observations, that she had been in contact since the eggs were laid.

The nest found by Tanner (1953) was unique in that eggs were clustered, with 6 tied together by gelatinous strands that formed a spiral chain (Stebbins 1949) and 2 others loose but still within the cluster. The nest's location on the upper surface of the log may be significant because, from that position, it would more likely receive added solar radiation. Two nests reported by Jockusch and Mahoney (1997) were also found in fir logs, but locations within the logs were not given. Location in the log may be important, particularly if beetle trailways are favored as nesting sites and if solar radiation is a factor affecting choice of nest site. Jockusch and Mahoney (1997) reported that the eggs they found were not together in a nest nor in a cluster, but scattered within an area of 10 cm. This suggests, based on the finding of Tanner (1953), that the nest may have been disturbed and did not represent a typical nesting

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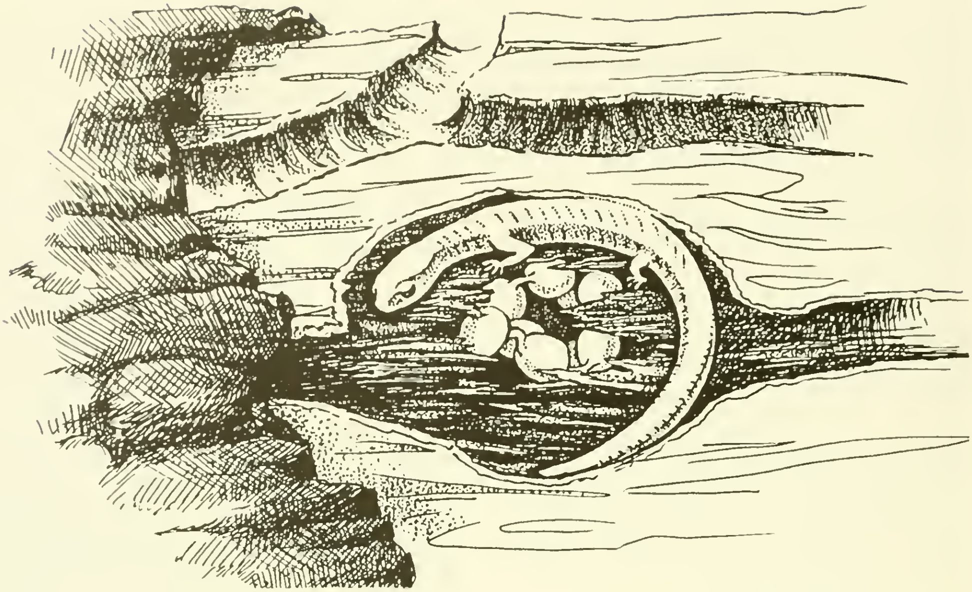

Fig. 1. Sketch simulating the nest of *Batrachoseps wrighti* observed in 1952 (Tanner 1953). Drawing by Randal Baker.

site, assuming that Tanner's nest was typical. Eggs laid in the laboratory, as reported by Stebbins and Lowe (1949) and Stebbins (1949), were also in clusters, tied together by gelatinous strands, and with only a few eggs unattached.

Laboratory studies involving reproduction in *B. wrighti* strongly indicate that brooding does not occur in the laboratory. Gravid females that have oviposited either with or without pituitary implants have shown no inclination to brood (Stebbins 1949). The question arises as to whether brooding occurs naturally in *B. wrighti*, or if the change from natural habitat to laboratory alters their behavior (Stebbins 1949, Jockush and Mahoney 1997). Although laboratory data are suggestive, the finding of a female in the nest with eggs (Tanner 1953) may indicate that under natural habitat conditions some *B. wrighti* females remain at the nest. This single observation does not suggest that either brooding or abandoning the nest occurs; it merely demonstrates that in this instance a female was at the nest. Whether the nest is soon abandoned, as suggested by Jockusch and Mahoney (1997), or is attended for a time, as indicated by Tanner (1953), must be determined by additional research.

From their observations Jockusch and Mahoney (1997) conclude that brooding in *B. wrighti* does not occur. Observations of the 3 nests mentioned (1 attended but not disturbed; 2 unattended but with indications of possible disturbances) suggest the evidence is not yet definitive. The attending female at the nest (Tanner 1953) was nestled in rotting wood near the eggs and did not move until collected. How long she had been in the nest with the eggs is unknown. However, the only embryo that developed from eggs taken from that nest in 1952 was compared to growth stages reported by Stebbins (1949). I suggested then that 1–2 wk might have elapsed since oviposition occurred, during which time the female possibly remained in the nest or nesting area. Some plethodontid females remain in the nest with their eggs during incubation, some remain for a time near the eggs, and others abandon the nesting area soon after oviposition (Bachmann 1984, Carreño and Harris 1998).

Speculations of Jockusch and Mahoney (1997) are seemingly an attempt based on limited data to bring the reproductive patterns of *B. wrighti* into close conformity with attenuate species of *Batrachoseps*. While some aspects may conform, it should be understood that *B.*

wrighti is morphologically different from *B. nigriventris* and other closely related attenuate species of *Batrachoseps* (Bishop 1937, Stebbins and Lowe 1949). In addition, it appears that *B. wrighti* reproduction differs from that of attenuate species in the following ways: (1) eggs are laid in spiral, beadlike clusters; (2) eggs are laid in single, not communal, nests; and (3) apparently, eggs are laid in rotting fir logs. Available data indicate that nesting occurs during May and June. A comprehensive research study should be conducted for *B. wrighti*, comparable to the detailed study of *B. nigriventris* (Jockusch and Mahoney 1997), to eliminate uncertainties and preclude further speculation.

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